Primates under Altered Living Conditions: Development and Conservation Potential of the Captive Lion-tailed Macaque *Macaca silenus* Population

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> ***"More than any other country of the world, Germany has contributed to opening up and broadening the channel that connects the forces of reason and spirit of the West with India. The homage of love that Germany gave today to a poet of the East on her own initiative certainly will still further deepen these relations by imbuing them with an intimate and personal character.***

Declaration of Independence

Herewith I certify that I have prepared and written my thesis independently and that I have not used any sources and aids other than those indicated by me. I also declare that I have not submitted the dissertation in this or any other form to any other institution as a dissertation.

Gleichen, 25 January 2023

Nilofer Begum

List of publications

This thesis is based on the following four peer-reviewed publications:

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Chapter 2

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Chapter 5

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A female lion-tailed macaque in its natural habitat in the Western Ghats, southern India.

Photo: Werner Kaumanns

Contents

List of abbreviations used in general introduction and general discussion

Abbreviation	**Full term**
AZA	Association of Zoos and Aquariums
EAZA	European Association of Zoos and Aquaria
EEP	European Endangered Species Programme; renamed to EAZA *Ex situ* programmes
GSMP	Global Species Management Plan
HIREC	Human-Induced Rapid Environmental Change
IUCN	International Union for Conservation of Nature
LTM	Lion-tailed Macaque
SSC	Species Survival Commission
SPARKS	Single Population Analysis and Records Keeping System
SSP	Species Survival Plan
WAZA	World Association of Zoos and Aquariums
ZIMS	Zoological Information Management System

Zusammenfassung

Die Studie bezieht sich auf eines der Hauptprobleme der „Conservation Biologie“ und ihrer Teildisziplin Zoobiologie: das langfristige Überleben von Tierpopulationen unter vom Menschen veränderten Lebensbedingungen. Angesichts des schlechten Status der Wildpopulationen sollen viele in Zoos gehaltene Populationen als Modelle, Ressourcen für Forschung und Bildung und vor allem als Reserven für die bedrohten Wildpopulationen dienen.

Die Studie untersucht Bartaffen (*Macaca silenus*). Ihre wilden und in Gefangenschaft lebenden Populationen sind bedroht, leben unter veränderten Bedingungen und bedürfen eines erhaltungsorientierten Managements. Dazu will die Studie einen Beitrag leisten. Sie konzentriert sich auf Bartaffen in Zoos und untersucht die Struktur und langfristige Entwicklung ihrer globalen historischen Population in Gefangenschaft. Sie untersucht ihr Potenzial, langfristig zu überleben und als Reserve zu dienen. Sie ist eine der größten und ältesten Primatenpopulationen in Gefangenschaft. Ihr internationales Zuchtbuch, das die Grundlage für diese Studie bildet, umfasst mehr als hundert Jahre und die gesamte Population mit fast 3000 Individuen in mehr als 300 Zoos. Die Population kann als Modell für andere Primatenarten dienen, die unter veränderten Bedingungen leben.

Die Studie, die in verschiedenen Veröffentlichungen dargestellt wird, gliedert sich in fünf Hauptteile:

- Erstellung einer aktualisierten Version des internationalen Zuchtbuchs, um die Studie auf vollständige und korrekte Daten stützen zu können, die bis 2018 aktualisiert sind.
- Beschreibung und Analyse der Entwicklung der Population in Bezug auf Populationsgröße, Geburten und Todesfälle.
- Analyse der individuellen Reproduktionsleistung der Weibchen im Hinblick auf mögliche Bedingungen, die die Fortpflanzung beeinflussen.
- Erarbeitung eines konzeptionellen und theoretischen Hintergrunds des Populationsmanagements.
- Erarbeitung von Perspektiven für das künftige Management der derzeitigen Gesamtpopulation.

Die Ergebnisse zeigen ein langsames, aber stetiges Populationswachstum, wobei die Zahl der Geburten nur geringfügig höher ist als die Zahl der Sterbefälle. Die Population blieb über mehrere Jahrzehnte ohne weitere Integration von in freier Wildbahn gefangenen Individuen bestehen. Sie wies - managementbedingt - Perioden des Rückgangs der Geburtenzahl und eine Abnahme der Populationsgröße auf. Letzteres ist auch im letzten Jahrzehnt zu beobachten. Die Kindersterblichkeit machte einen großen Teil der Gesamtsterblichkeit aus und ist höher als in freier Wildbahn.

Ein großer Teil der Weibchen und ein noch größerer Teil der Männchen trugen nicht zur Reproduktion in der Population bei. Im Gegensatz zu dem, was für wildlebende Bartaffen beschrieben wird, wurde eine große Varianz in der individuellen Reproduktionsleistung gefunden. Eine Analyse der Größe und Zusammensetzung der Gruppen (Anzahl der Individuen pro Standort) zeigte, dass die meisten viel kleiner waren als die in der freien Wildbahn beschriebenen Gruppen. Die Weibchen in den wenigen größeren Gruppen erwiesen sich als produktiver, obwohl sie möglicherweise Perioden der Geburtenkontrolle durchlaufen haben. Viele Gruppen waren wahrscheinlich sozial instabil, da die Weibchen entfernt und in andere Gruppen transferiert wurden. In freier Wildbahn bleiben Bartaffenweibchen lebenslang in ihrer Geburtsgruppe.

Es wird davon ausgegangen, dass diese Merkmale auf Populationsebene und über den gesamten Zeitraum ihres Bestehens zu Diskrepanzen mit arttypischen Anpassungen wie dem "female-bonded" Sozialsystem geführt haben. Letzteres wird wie bei anderen Makaken als ein Schlüsselmerkmal der Art angesehen. Größe und Struktur der meisten Gruppen in der globalen historischen Population boten nicht die Voraussetzungen für die Verwirklichung dieses arttypischen Sozialsystems und könnten daher zu ungünstigen Reproduktionsbedingungen beigetragen haben.

Die Tatsache, dass die in Gefangenschaft lebende Population des Bartaffen über mehrere Jahrzehnte hinweg durch Nachzucht erhalten werden konnte, deutet zwar auf ein Potenzial für den langfristigen Fortbestand der Population hin, doch scheint die Persistenz der Population ohne signifikante Verbesserungen im Management unwahrscheinlich. Durch ein verbessertes Verhaltens - und Sozialmanagement soll eine höhere Produktivität und der Erhalt des Zuchtpotenzials erreicht werden. Es sollte den enormen Verlust an (potenzieller) phänotypischer und genetischer Vielfalt verringern, der durch die geringe Produktivität

induziert wird. Ein Wechsel des Managementparadigmas und ein breiterer Ansatz mit stärkerer Betonung der individuellen Phänotypen, ihrer Lebensgeschichte und der Grundannahme, der life-history theory, dass Tiere „für die Fortpflanzung gebaut sind“ (Kapitel 5).
Die Studie zeigt, dass im Hinblick auf die Gesamtentwicklung und die Reproduktionsmuster in der globalen historischen Population des Bartaffen mehr Koordination, Orientierung und Kontrolle der Auswirkungen von Managementmaßnahmen sowohl für die globale als auch für die Teilpopulationen erforderlich sind. Es weist auf entsprechende Defizite im Design und in der Durchführung der Zuchtprogramme hin. Adaptives Management *sensu* Walters and Hilborn (1978) sollte realisiert werden - basierend auf einer umfassenderen und aktualisierten Berücksichtigung der Biologie dieser bedrohten Art.

Die Studie musste sich auf Zuchtbuchdaten stützen, deren Möglichkeiten zur statistischen Auswertung und zur Analyse von proximaten Aspekten begrenzt sind. Sie ermöglichen jedoch die Gewinnung von Informationen, die für die Entwicklung von Managementprogrammen, die für den Fortbestand der in Gefangenschaft lebenden Population und ihr Potenzial als Reservat unterstützen, unerlässlich sind.

Summary

The study refers to one of the main problems of conservation biology and its sub-discipline, zoo biology: the long-term persistence of animal populations under human-induced altered living conditions. With reference to the poor status of wild populations, many captive populations in zoos are supposed to serve as models, resources for research and education, and especially as reserves for threatened wild populations.

The study investigates lion-tailed macaques (*Macaca silenus*). Their wild and captive populations are threatened, live under altered conditions, and require conservation-oriented management. The study intends to contribute there. It focuses on lion-tailed macaques in zoos and investigates the structure and long-term development of their global historical captive population. It assesses its potential to achieve long-term persistence and to serve as a reserve. It is one of the largest and oldest captive primate populations. Its international studbook, providing the database for this study, covers more than a hundred years and the complete population with almost 3000 individuals in more than 300 zoos. The population can serve as a model for other primate species living under altered conditions.

Reflected in various publications, the study is organised into five main parts:

- Establishment of an updated version of the international studbook to be able to base the study on completed and correct data updated till 2018.
- Description and analysis of the development of the population with reference to population size, births, and deaths.
- Analysis of individual reproductive output in the females with reference to possible conditions to influence breeding.
- Elaborating a conceptual and theoretical background of population management.
- Elaborating perspectives for the future management of the current global population.

The main results reveal a slow but steady population growth, with the number of births only slightly higher than the number of deaths. The population persisted without further integration of wild-caught individuals over several decades. It revealed – management-induced – periods of decrease in the number of births and a decrease in population size. The latter is also found in the last decade. Infant mortality constituted a large proportion of overall mortality and is higher than that found in the wild.

A large proportion of the females and even a larger proportion of the males did not contribute to reproduction in the population. Contrary to what is described for wild lion-tailed macaques, a large variance in individual reproductive output was found. An analysis of the size and composition of the groups (number of individuals per location as a proxy) showed that most of the groups were much smaller than what is known from groups in the wild. The females in the few larger groups were found to be more productive, although they might have undergone periods of birth control. Many groups were likely to be socially unstable due to the removal of females and transfers to other groups. In the wild, female lion-tailed macaques remain in their natal groups lifelong.

It is assumed that these features on the population level and over its full period of existence induced mismatches with species-typical adaptations like a female-bonded social system. The latter is regarded as a key trait of the species, like for other macaques. The size and structure of most of the groups in the global historical population did not provide the conditions to realise this species-typical social system and, therefore, may have provided poor breeding conditions.

The existence of the captive population of the lion-tailed macaque over several decades via breeding indicates a potential for long-term persistence. The latter, however, seems unlikely without significant improvements in management. It has to achieve more breeding and the preservation of the breeding potential by an improved behavioural and social management. It should decrease the enormous loss of (potential) phenotypic and genetic diversity induced by low productivity. A change of management paradigm and a broader approach with more emphasis on the individual phenotypes, and their life histories, are indicated. It also should consider the basic assumption of life-history theory that animals are "designed for breeding" (Chapter 5).

The study indicates that with reference to the overall development and the patterns of reproduction in the global historical population of the lion-tailed macaque, more coordination, orientation, and control of the effects of management measures for the global as well as for the subpopulations is needed. It reveals corresponding deficits in the design and execution of the breeding programmes. Adaptive management *sensu* Walters and Hilborn (1978) should be

realised – based on a more comprehensive and updated consideration of the biology of this endangered species.

The study had to be based on studbook data with a limited potential for statistical treatment and to analyse proximate conditions. They, however, allow gaining information that is essential for the development of management programmes that support the persistence of the captive population and its potential as a reserve.

Chapter 1: General Introduction

The study investigates the captive population of the lion-tailed macaque *Macaca silenus*. Its wild and captive populations are threatened, live under altered conditions, and require conservation-oriented management (see Singh et al. 2020). The study investigates the structure and long-term development of the global historical captive population of the species. The population is supposed to serve as a reserve and model for the threatened wild population. The captive population should be able to persist over long time periods via births into the population. Lion-tailed macaques are kept in zoos since more than one hundred years. The population persists over several decades without introducing wild-caught individuals but reveals unsatisfactory population growth and breeding problems.

Evidently, the life of the members of a captive population is influenced by their (artificial) living conditions and their husbandry and management programmes. Whether captive populations are comparable in a strict sense and can reveal similar patterns of development and productivity to those of wild populations has to be considered critically. Successful reintroductions of specimens of a number of endangered species kept in zoos (e.g., black-footed ferret *Mustela nigripes*, Seal et al. 1989; Arabian oryx *Oryx leucoryx*, Stanley Price 1989; California condor *Gymnogyps californianus*, Snyder and Snyder 2000), including the golden lion tamarin *Leontopithecus rosalia* (Kleiman and Mallinson 1998; Kierulff et al. 2012), have been reported. However, sustainability problems, as described for many captive populations, do not allow the establishment of reserves for many, if not most, species (see Stanley Price and Fa 2007; Conde et al. 2013; Lacy 2013).

So far, reintroductions of captive-born lion-tailed macaques into their natural habitat have not been realised. With reference to the current status of the population in the wild, they might become necessary (see Molur et al. 2003; Singh et al. 2020). There are about 4000 lion-tailed macaques left in the wild. With about 516 individuals, the captive population constitutes about 11% of the total population – a number of individuals that might be critical for the survival of the species.

Management-induced, the North American subpopulation in the last decades decreased to a small number of non-breeding individuals. The European subpopulation, now constituting about 62% of the global population, reveals, also management-induced, decreasing numbers of births and decreasing population size. The current status of the global captive population of the lion-tailed macaque, therefore, is labile and requires management efforts to support its persistence and its potential to contribute to the survival of the species (see Kaumanns et al. 2013; Kaumanns and Singh 2015). By analysing the history and the development of the global historical population, our study intends to provide materials for corresponding management programmes.

The theoretical background of the study refers to concepts of population ecology and conservation biology with special emphasis on its sub-discipline, zoo biology. The genetics of small populations and life-history theory also provide important concepts.

Background of the study

1.1 Population ecology, conservation biology, zoo biology

The study deals with a captive population of a primate species. Captive populations are virtual populations consisting of a number of widely distributed individuals and isolated breeding units. Population dynamics e.g., the exchange of breeding males, is induced by management procedures.

A natural population, according to Turchin (2003, p.19), is "a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and migration behaviour, and in which population changes are largely determined by birth and death processes." Population ecology is the discipline that investigates the processes in natural populations. Population ecologists are interested in population-level properties such as persistence, resilience, and patterns of abundance over space and time. In order to answer questions about populations, ecologists have derived a variety of predictive models, the use of which depends on the life-history of the organisms (Rockwood 2006).

Due to the increasingly fragmented status of natural habitats, populations are now more likely to be small, restricted in distribution, and increasingly isolated from each other. As a result of the increasingly threatened status of nature, ecologists stressed the importance of the spatial context in populations, communities, and ecosystems. Allee (1931, 'Allee effect') drew attention to the possibility of a positive relationship between aspects of fitness and population size. Stephens et al. (1999, p.186) defined the Allee effect as "a positive relationship between any component of individual fitness and either numbers or density of conspecifics". Low population size or density can lead to a decline in individual fitness (Allee 1931, 'Allee effect'), resulting in critical population thresholds (see Courchamp et al. 2008). Allee effects can be a threat for zoo populations (Swaisgood and Schulte 2010).

The perception of accelerated extinction rates in natural populations (Myers 1979; Wilson 1988) led to a discipline "conservation biology" as the science of scarcity and diversity (Soulé 1985). It integrates concepts and tools of ecology, biogeography, demography, life history theory, physiology, genetics, and many applied disciplines such as wildlife management, forestry, and captive breeding (Frankel and Soulé 1981).

Conservation biologists intend to manage threats to avoid the biological extinction of populations, species, and clades. It can include non-natural populations. Zoo biology, with its focus on wild animals living under the altered conditions in zoos, is regarded as a sub-discipline of conservation biology.

With the increased awareness of species extinction in fragmented and altered habitats, population ecologists and – even more focused – conservationists were interested in clarifying issues related to the size of populations of endangered species and their viability (see also 'Allee effect' above). These included the species-area relationship and the capacity of habitats to ensure the requirements of the species. Diamond (1975) noted that different species require different minimum areas to sustain a population increase. This led to the concepts of the minimum viable population (MVP) and population viability analysis (PVA). The minimal population size and minimal area size are evidently also important topics for zoo biologists since space and "carrying capacity" are extremely limited. The problem in zoos is growing with an increase in the number of threatened species that would need 'reserves'. Soulé et al. (1986) proposed the Noah's Ark approach that projected management perspectives, including cryo-technology, for the next 200 years.

The concept of the minimum viable population size was originally defined by Shaffer (1978, 1981) as the smallest number of individuals required for an isolated population to persist (at some predefined 'high' probability) for some 'long' time into the future. Shaffer's study pointed to the need to define the minimum size of a given population of species for its survival for a long time, mainly referring to the fragmented status of habitats (Shaffer 1978, 1981; Quammen 2004). An earlier approach to deal with fragmented populations by regarding them as a whole ("population of populations") and managing them as a "metapopulation" was developed by Levins (1969, 1970). It was regarded as a key concept in understanding the population dynamics in fragmented habitats (Gilpin and Diamond 1976, 1980; Gilpin and Soulé 1986; Quammen 2004) and became one of the fastest growing research areas in population, community, landscape, and conservation biology.

Evidently, the metapopulation concept is important for the work in zoos and, in particular, for breeding programmes. Per definition, the concept virtually combines dispersed sub-populations and zoo colonies of threatened species and intends to manage them in larger units like countries, subcontinents, or continents. Global management is attempted in a few cases. Interactive management between captive and wild populations is attempted and realised for some species. The study species, the lion-tailed macaque, was one of the first species under consideration for a global *in situ* – *ex situ* conservation management (Heltne 1985; Singh et al. 2009). Our study is an outcome of these efforts.

The application of genetics to conservation in a more general context took place during the 1980s, with mainly three publications that established the foundation for applying the principles of genetics to conservation biology (Soulé and Wilcox 1980; Frankel and Soulé 1981; Schonewald-Cox et al. 1983). The pioneers of conservation biology, like Soulé and others, have developed their concepts independent of zoo populations, but they often used zoo populations because they provided good examples for the kind of threatened and altered natural populations they were investigating. Meetings and workshops were organised and attended by zoo and conservation biologists and geneticists working on wild populations and animals under human care. Research on and the preservation of small, isolated, altered populations with their demographic and genetic problems was a key topic. The emphasis on the genetics of small populations was adopted by zoo biologists and regarded as the key aspect in managing the (small and altered) zoo populations. They were used as leading concepts for defining the goals and structures of the main international breeding programmes like SSP (Species Survival Plan in North America) and EEP (European Endangered Species Programme) and influenced the development of captive populations in zoos.

The genetic problems potentially faced by small populations that can increase their risk of extinction via inbreeding and genetic drift (Frankel and Soulé 1981; Frankham 1995, 1999) have constituted a central topic for conservation biology, particularly in zoo biology. Franklin

(1980) suggested that a minimum effective population size of 50 would be required to avoid inbreeding depression in the short term, and an effective population size of 500 would prevent long-term erosion of genetic variability by drift. This formed the idea of the “rule of 50/500” (Soulé and Wilcox 1980; Quammen 2004). The suitability of its application, however, is under much discussion, especially regarding its generality across species and populations (Traill et al. 2010; Brook et al. 2011; Flather et al. 2011a, b). Recently, Frankham et al. (2014) proposed to increase the 50/500 values to at least 100/1000; and suggested that an effective size of at least 1000 individuals would be needed to retain evolutionary potential. According to Flather et al. (2011a), there is no single ‘magic’ population size that can ensure population persistence and “that multiple populations totalling thousands (not hundreds) of individuals will be needed to ensure long-term persistence.” The classic rule is, however, still relevant in conservation practices, for example, for determining threatened species categories by the IUCN and as a tool to communicate to policymakers about the urgency of actions needed (Traill et al. 2010). The concept of MVP and the “rule of 50/500” were important details in Soulé et al.’s (1986) influential paper that has been used to set standards/ “rule of thumb” for captive breeding programmes. The concept and the rule are still in use but whether they really will turn out to be appropriate seems to be undecided. For the captive population of the lion-tailed macaque in North American zoos, Conway (1985) suggested, “we need to provide space for an effective breeding population of about 500 lion-tails in captivity” (Conway 1985, p.5). The current captive population as of 2018 comprises the suggested number (n = 516) of individuals in zoos worldwide, with a dominant core population of 322 individuals in European zoos. The present study, however, shows the data and development behind this current size and points to a potential loss of genetic and phenotypic diversity (see **Chapter 2**). Furthermore, a potentially much lower effective population size is hidden (see Sliwa and Begum 2019).

1.2 From populations to individuals, individual-based ecology

Conservation biology has been predominantly system-oriented, i.e., at the level of ecosystems and landscapes (Franklin 1993) and did not focus on the individuals living in these systems. However, populations are composed of individuals, and the dynamics of populations that affect their viability and hence “fitness” are greatly affected by the behaviour of individuals and their life histories (Lomnicki 1980).

Most studies in conservation and management used ecological modelling focused on the population and community level and treated individual conspecifics as biologically equivalent (as discussed, for example, in Lomnicki 1978, 1999; Bolnick et al. 2003, 2011). According to evolutionary theory, natural populations consist of phenotypically diverse individuals (Darwin 1859) that exhibit variation in their demographic parameters and intra- and interspecific interactions (Lott 1991; Bolnick et al. 2011). Darwin (1859) identified the variation amongst individuals as the raw material for natural selection, and therefore, it is a key focus of evolutionary theory and phenotype-oriented management approaches (Watters et al. 2003; Carroll and Watters 2008; Watters et al. 2017). Several authors noted that individual differences could have significant ecological effects (Lomnicki 1978, 1980, 1999; Kaiser 1979; Huston et al. 1988; Ricklefs and Wikelski 2002; Dall et al. 2012). An ecology based on individuals was pioneered by Lomnicki (1978) and Kaiser (1979) and elaborated by a number of authors such as Grimm and Railsback (2005), Goss-Custard and Stillman (2008), and Stillmann et al. (2015). The role of the individual animal's behaviour in species conservation has been put forward by several authors (Anthony and Blumstein 2000; Sutherland and Gosling 2000; Singh and Kaumanns 2005) and is reportedly particularly important in smaller and fragmented animal populations (Gosling 2003). For the integration of the individual and their behaviour into conservation-oriented management, some authors point to the necessity to refer to evolutionary biology (Kaumanns and Singh 2015; Schulte-Hostedde and Mastromonaco 2015), especially to life-history theory (Stearns 1976, 1977, 1992, 2000; Ricklefs 1991; Ricklefs and Wikelski 2002) and individual-based phenotype-oriented management concepts (Watters et al. 2003, Carroll and Watters 2008, Stillmann et al. 2015, "individual-based ecology").

A focus on individual animals in zoos was propagated in the early period of zoo biology by its pioneer Heini Hediger but got less emphasis in the context of captive population management. Individuals were rather regarded as 'gene carriers' and lesser under the perspective of "individual phenotypes" (Kaumanns and Singh 2015). **In Chapter 5, these aspects are elaborated.**

1.3 Altered living conditions

Our study species, the lion-tailed macaque, lives under altered conditions both in its natural habitat and under captive conditions. An investigation of the development, productivity, and potential for persistence of the global captive population has to consider this aspect.

Altered living conditions threaten the survival of many animal and plant species. They are investigated in many studies with a focus on wild populations. Studies on altered living conditions in captive animals and captive populations, respectively, are rarer, except in the context of enrichment and welfare projects (see Shepherdson et al. 1998; Novak et al. 2006; for an overview, see Hutchins et al. 2019). Living conditions in zoos, especially for mammals and birds, usually are extremely altered in comparison to wild conditions. A number of studies have shown the influence of captive environment, for example, on the behaviour of individual animals (for a review, see Carlstead 1996).

The following section provides an overview of the topic.

1.3.1 Wild populations under altered living conditions

Populations living under altered conditions often are small, isolated, fragmented, and threatened by extinction. They are vulnerable to extinction, which may result from the ‘evil quartet’ of habitat loss and fragmentation, over-exploitation, introduced species and chains of extinctions (Diamond 1984; Caughley 1994; Purvis et al. 2000; May 2010) as well as environmental pollution, disease, parasitism, and global climate change (e.g., Gibbons et al. 2000) and the inherent vulnerability of small populations (stochastic processes; Shaffer 1981; Gilpin and Soulé 1986; Fischer and Lindenmayer 2007). Many of the described changes are human induced, which rapidly and extensively alter the living conditions of animals and plants such that they are different from those in the evolutionary history of a species. Sih et al. (2011) established the term HIREC (human-induced rapid environmental change) to focus on conservation-related problems and initiated many studies. According to the authors, a key to understanding the responses of species to HIREC is the match versus mismatch between the past environment in which the species evolved and the present human-altered conditions.

The survival of populations is regarded as a key problem of conservation biology (Soulé 1985). Caughley (1994) noted that conservation biologists use two paradigms for understanding the extinction of populations, the “small population paradigm” and the “declining population paradigm.” Whereas the small population paradigm emphasises ‘smallness’ itself as an ultimate cause of extinction, especially through the loss of genetic diversity, the declining population paradigm emphasises the factors causing populations to decline in the first place. Caughley (1994) argued that the paradigms were largely used in isolation of one another. An integration of the two might better achieve effective management of populations (Boyce 2002; Armstrong 2005). In more recent papers, it is proposed that an approach that recognises the importance of the declining population paradigm and combines both paradigms might provide the best results (Conway 1995; Caughley and Gunn 1996; Boyce 2002; Armstrong 2005; Armstrong and Seddon 2008). **In chapter 5, the need for an integrated approach is indicated.**

A special case of altered living conditions is induced by the fragmentation of continuous natural landscapes. It contributes to the increasing loss of biological diversity (Wilcox and Murphy 1985). Fragmentation can induce increased mortality of individuals moving between patches, lower recolonisation rates of empty patches, and reduced local population sizes resulting in increased susceptibility to extinction (Fahrig and Merriam 1994). Fischer and Lindenmayer (2007) provide cases for the effects of fragmentation. The consequences of habitat fragmentation have become a key issue in conservation biology (e.g., Soulé 1986). A review by Fahrig (2003) on the effects of habitat fragmentation on various taxa consisting of birds, insects, small mammals, plants, and aquatic invertebrates, reported that all these taxa were negatively affected by habitat fragmentation.

For primate populations, the impact of habitat degradation, fragmentation, and loss is increasingly documented (e.g., Marsh 2003; Arroyo-Rodriguez and Dias 2010; Marsh and Chapman 2013; Estrada et al. 2017). Some long-term responses of primate communities to logging include lower – species richness, abundance, and breeding rates (Skorupa 1986; Johns 1992; Struhsaker 1997; Chapman et al. 2018). Arboreal (Eppley et al. 2022), habitat specialist, and frugivorous primates (see Rode et al. 2006; de Almeida-Rocha et al. 2017) with small ranges and low population sizes (Purvis et al. 2000), like the lion-tailed macaque might be particularly vulnerable to habitat disturbance (see Sushma et al. 2014; Kumar et al. 2018).

The study species lion-tailed macaque (*Macaca silenus*), endemic to the rainforests of the Western Ghats in southern India, is endangered due to continued habitat destruction and fragmentation (Singh et al. 2020). Hunting is a second major threat in certain parts of its range

(Kumara and Singh 2004a). The total population has been estimated to be about 4000 individuals fragmented into 47 subpopulations (Molur et al. 2003; Singh et al. 2020). The population is declining, and the species is locally extinct in some areas (Kumara and Singh 2004a, b; Kumara and Sinha 2009). Conditions that allow population viability occur only in a few regions (Kumara and Sinha 2009; Singh et al. 2020). The species occurs along narrow strips of rainforests in the Western Ghats Mountain range and has an area of occupancy of less than 2500 km^2 (Molur et al. 2003). A number of exploitative activities like commercial plantations of, for example, tea, coffee, rubber, and logging, as well as the development of hydroelectric dams and power generation, have forced the lion-tailed macaques to inhabit fragmented, degraded, and poor-quality habitats only (Kumar et al. 1995a; Kumara and Sinha 2009; Singh et al. 2009). Some patches of degraded areas have lost their rainforest characteristics (Kumar 1985). Construction of roads and immigration of millions of people to assist the developmental projects and later their settlement in the areas (Kumar 1985; Chandran 1997) has intensified the problems faced by the macaques like accidents, increased conflicts with humans and prevalence of parasites (see Singh et al. 2001; Hussain et al. 2013; Jeganathan et al. 2018a, b). The history of the loss of the rainforests in the Western Ghats dates to the 1860s following the British occupation and was possibly earlier than the rainforest loss in most of southeast Asia (see Kumar 1985; Chandran 1997). Large-scale felling for the establishment of tea plantations and monoculture plantations of timber and Eucalyptus were largely responsible for the massive early transformation of the forests (Chandran 1997). A loss of about 40% of the forest cover and an increase of four times the number of fragments have been reported even between 1920 and 1990 (Menon and Bawa 1997). The lion-tailed macaque is adapted to a highly arboreal life, living in the tropical evergreen climax rainforest (Singh et al. 1997). As the species does not use tea plantations, roadside trees, or non-canopy matrices for dispersal (Umapathy 1998), groups inhabiting the fragments have been isolated since decades (see Singh et al. 2009). It is known that species that cannot use the surrounding matrix to move between fragments are particularly sensitive to the effects of fragmentation (Kumar et al. 1995a). Managing the population of lion-tailed macaque in isolated and highly altered rainforest fragments, therefore, is the major conservation challenge for this species (Singh 2019). Management recommendations suggested in the last four decades (Kumar et al. 1995a; Molur et al. 2003; Kumara and Sinha 2009; Singh et al. 2009; Umapathy et al. 2011; Kumara et al. 2014; Singh 2019; Singh et al. 2020) included a) long-term monitoring of macaque groups, b) identification of all viable populations and metapopulations, and their legal protection, c) resource quality enhancement in degraded habitats, d) linking fragments with narrow corridors allowing male migration (see below “Study species”), e) exchanging males between fragments, f) linking canopies via wooden bridges to reduce road kills, and f) the establishment of a self-sustaining “reserve” population in zoos (*ex situ*) to reinforce the endangered wild population when needed, that would also serve as a source for research, education, and to raise funds to support conservation projects.

1.3.2 Altered living conditions in zoos – Zoo biology

Living conditions in zoos

Wild animals living in zoos have to cope with altered living conditions that differ from the conditions in their natural habitats (e.g., McPhee and Carlstead 2010). Altered living conditions in zoos include, for instance, reduced physical and spatial conditions, untypical demographic structures and social conditions, modified diet and foraging opportunities, interactions with humans, exposure to chemicals and noise, and the overall predictability of everyday routine life (Eisenberg and Kleiman 1977; Bassett and Buchanan-Smith 2007; Morgan and Tromborg 2007; Mason et al. 2013). They lack various complexities and variations of natural habitats. The conditions are sometimes similar to the human-induced altered conditions in fragmented and degraded wild habitats (Kaumanns et al. 2008). Mason et al. (2013) provide a review of altered living conditions in zoos and draw parallels with HIREC in the wild (see above). They, for instance, point to mismatches that can emerge between the species’ ancestral environment and present captive living conditions, which can result in coping problems. In the present study, we identify a number of (demographic) conditions that may lead to mismatches with species-typical adaptations of the lion-tailed macaque. Following Schulte-Hostedde and Mastromonaco (2015), they might contribute to low productivity at individual and population levels (**see Chapter 3**).

Much of the history of the global historical captive population of the lion-tailed macaque is paralleled by the history of zoo biology, the biological discipline that deals with wild animals and their living conditions in zoos. On the level of individual zoos and national husbandry and management approaches, explicit and non-explicit concepts of zoo biologists influenced the way zoo animals – including lion-tailed macaques – were kept. To inform about this background, a rough overview of the development and important topics of zoo biology is provided. The pioneer of zoo biology was Heine Hediger, a Swiss zoo director.

Dealing with altered conditions in zoos: Hediger's approach to zoo biology

According to Hediger (1942, 1950), the founder of "Zoo Biology", a key component of the work in zoos is dealing with the altered living conditions in zoos *scientifically*. The author described zoo biology as a multidisciplinary field of applied biology within which the various disciplines (for example, zoology, comparative psychology, ecology, pathology) should function interactively towards dealing with three main clusters of problems: space, nutrition, and the animal man relationship (see Hodges et al. 1995). Hediger's early outline of a zoo biology mainly focused on the ethical, scientific, and practical questions resulting from the special conditions of the captive environments. According to Hediger (1969), zoo biology embraces everything in the zoo which is biologically relevant. In his many books and articles (e.g., Hediger 1942, 1950, 1969, 1982), he recognised that conditions in zoos might not meet the biological and psychological needs of wild animals and that captive animal keeping needs to be based on an understanding of the natural history of the species concerned (see also Chrulew 2020). Hediger referred to the concepts of, for example, territoriality and flight distance, the importance of physiological and psychological space, consideration for the quality and not only the amount of space, and emphasised species-appropriate social organisation, mating patterns, natural diet, and food presentation. Hediger's theoretical view originated from Jakob von Uexküll's *Umwelt-theory* (von Uexküll 1957), and he contributed to putting the *theory* into practice – by attempting to reconstruct the individual animal's meaningful *subjective* 'world' or 'Umwelt' in a zoo (Chrulew 2018, 2020). Aspects of the individual's behaviour, physiology, reproduction, and health were in focus. Till about half of the 20th century, there was no active incorporation of contemporary field studies in the management of wild animals in zoos. Aspects of poor housing, physical and psychological problems of animals in zoos, and animal welfare were not yet fully considered by legislators, keepers, or the public (see Stevens and McAlister 2003; Fa et al. 2011). Mortality was high, and breeding was rare (see Yerkes 1925; Maple 1979; Knowles 2003; Kreger and Hutchins 2010). Hediger's foundational work, especially with its 'zoocentric' approach, was, therefore, considered a major paradigm shift for the work in zoos at that time (Seidensticker and Forthman 1998). Although many of his proposals remained unrealised for years (see Seidensticker and Forthman 1998), they provided an important foundation for animal rights and welfare considerations in the later decades (Powell and Watters 2017). Until about the 1960s, the approach to managing animals in captivity largely referred to basic keeping systems such as exhibit areas, housing, restraint, diets, survival and longevity of animals and methods of breeding a species in individual zoos (see Crandall 1964; Kleiman 1996a). The particular roles of zoos in the conservation of nature were not yet focused on (see Hodges et al. 1995).

Captive population management

Due to the threatened status of nature, from the 1970s onwards, a change of paradigm for the work in zoos led to a new thinking in terms of populations above the level of individual zoos. As a result, (small) populations got into the focus of zoo biology and zoos shifted away from reliance on continued collection from the wild to captive propagation and management. "The purpose of population management is to ensure that populations of species of our choosing are available, healthy, and viable for the foreseeable future." (Ballou et al. 2010, p.219). Maintaining long-term viable populations was and is a key goal of captive population management programmes. Zoo populations were proposed to serve as reserves for threatened populations in the wild. Currently, however, due to sustainability problems in many populations, other functions like education are emphasised more. For an overview of the topics, approaches, and methods of modern zoo biology, see Kleiman et al. (2010).

The scientific background for modern, by now, population-oriented zoo biology was oriented towards the biology/genetics of small populations (Caughley 1994; Frankham 1995). It strongly considered the vulnerability of small, isolated populations in zoos as that of the small, fragmented populations in the wild. The risks to extinction were perceived as mainly stochastic and a consequence of genetic processes. It is assumed that genetic variation is the basis for adaptive evolution and must be retained to maintain the population's potential to adapt to environmental change (e.g., Levins 1968; Frankham et al. 2002). Captive populations were consequently managed within a paradigm that aimed at maintaining demographic stability and genetic diversity over a defined period of time (Soulé et al. 1986). Soulé et al. (1986) proposed a "millennium ark" model for zoos to establish large viable populations of about 2,000 species of large, terrestrial vertebrates that would be extinct if not bred in captivity. They suggested that the main goal of captive breeding should be the "maintenance of 90% of the genetic variation in the source (wild) population over a period of 200 years", with a founder group of at least more than "20 (effective) individuals". For an elaborated description of the now modified and commonly applied rule of thumb (90%/100 years) for captive population management, see Ballou et al. (2010).

The population management approach, as described above, is based on the "small population paradigm" used in conservation biology, which deals with the effect of smallness on the persistence of a population (Caughley 1994). The application of the paradigm is mainly realised via the exchange of genetically relevant individuals between institutions, modification of demographic structures within institutions and on a population level and attempts to breed specific individuals. They are supposed to optimise the genetic constitution of the population. The management has been facilitated by the development and widespread use of special software for data recording (e.g., SPARKS) and to analyse genetic and demographic parameters (e.g., PMx). The small population paradigm has been adopted by most breeding programmes for diverse taxa and populations in captivity (Montgomery et al. 1997; Ballou et al. 2010; Frankham et al. 2010). In most of these programmes, the production of individuals ("gene carriers") that fit with the attempted genetic diversity is an important goal of management (Ballou and Lacy 1995; Ballou and Traylor-Holzer 2011).

With this background, captive population management, overall, is executed in a highly standardised and strictly defined approach. It, however, was found to be in conflict with the day-to-day husbandry systems in zoos. Husbandry, housing, social grouping, nutrition, veterinary care, etc., are often specific to species and institutions (see Eisenberg and Kleiman 1977). Expertise in these aspects is derived from the personal experience of curators and keepers and a number of research areas like behavioural ecology, feeding ecology, reproductive biology, physiology, and knowledge of adaptive life-history patterning of the species (see also Powell and Watters 2017). The recommendations are forwarded in husbandry manuals and best practice guidelines for many species. They are often difficult to integrate into a population management planning that is biased towards concepts of the biology of small populations and genotype-oriented management. According to Lacy (2013), an integration of aspects such as behavioural variation, reproductive patterns, mate choice behaviours, parental care, disease resistance, and physiological responsiveness to environmental cues in population management needs to be considered more. The author emphasises the need to do this under the umbrella of pedigree-based management. **For a discussion of this approach, see chapter 5.**

The validity of the small population paradigm for the management of *captive* populations is not discussed as elaborately as it is done for *natural* populations (see Caughley 1994; Caro and Laurenson 1994; Asquith 2001). A number of authors (Kleiman 1992; Lindburg and Fitch-Snyder 1994; Schreiber et al. 1993; Wielebnowski 1998; Martin and Shepherdson 2012), however, point to the strong emphasis of the approach towards genetic management but also to the disregard of aspects of the captive environment and adaptive behaviours that may be important for the long-term survival of populations. The pairing of individuals based on genetic criteria alone, for instance, can impose monogamy and minimise sexual selection and has been considered to contribute to reproductive failure (see Chargé et al. 2014; Schulte-Hostedde and Mastromonaco 2015; Sorci et al. 2021). Seidensticker and Forthman (1998, p.25), for instance, argue, “it is not enough to produce and maintain genetically diverse offspring, we must also produce and maintain behaviourally competent animals that can thrive in the wild”. Kleiman (1996b, p.378), also, in the context of behaviour, especially associated with reproduction, noted that “a gorilla, *Gorilla gorilla* that cannot mate, care for its young, or socialise with other gorillas, is in fact, no gorilla at all”. **Chapter 5 discusses and proposes a management paradigm that considers these aspects.**

Back to individuals: Animal welfare, environmental enrichment

Opposed to a management that predominantly considered the individual’s contribution to the population’s genetic structure, issues about the individuals’ quality of life and their captive environments emerged (Shepherdson et al. 1998). As elaborated by Powell and Watters (2017), they were forwarded by “animal welfare” movements and the public in Europe and the USA, referring to the well-being (and suffering) of animals (wild or domesticated) kept under (possibly) suboptimal conditions, especially, in laboratories, zoos, and farms (see Brambell 1965; Dawkins 1980; Duncan 2006). According to the authors, the zoos themselves, and not the least zookeepers, also increasingly considered welfare matters (see above). It seems that an increased concern for at least aspects of the ‘real life’ of individual animals was “rediscovered” – possibly also with reference to the widespread breeding problems in many programmes (see Powell et al. 2019). Dealing with “welfare” issues requires investigating scientifically the conditions under which captive animals live – one of the basic principles Hediger (1969, 1982) propagated. Since the 1990s, “environmental” or “behavioural” enrichment” measures and programmes have been regarded as means of choice to improve welfare (see Shepherdson et al.

1998). Corresponding publications and projects are growing (see Young 2003; Kleiman et al. 2010; Maple and Perdue 2013). For the role of stress in animal welfare, see Broom and Johnson (2019). Some authors have even "upgraded" these fields of work and especially the topic of animal welfare, to "sciences" (see Maple 2007; Powell and Watters 2017), and it seems that it tends to "displace" the function and importance of "ordinary" husbandry and management. This trend seems contradictory to Hediger's broad approach, which basically proposed considering the full spectrum of natural conditions under which wild animals evolved and lived. Various authors, indeed, emphasise the need to integrate enrichment measures into general husbandry and management (Mellen and Shepherdson 1997; Mellen and MacPhee 2001; Coe and Dykstra 2010).

Enrichment and animal welfare concepts have been influenced by approaches and concepts of early comparative psychology and behaviourism, respectively, as represented, for example, by Watson (1928) and Skinner (1974). Guided by a rigid research paradigm, these researchers carried out their experimental studies (e.g., on learning) using animals kept under strongly controlled and often "barren" conditions that explicitly ignored species differences and corresponding adaptations (see Maple 1979; Shepherdson 1998; Mellen and MacPhee 2001). The behaviouristic approach of animal learning was based on operant conditioning techniques and assumed that the processes involved in learning were identical in all species (e.g., Skinner 1938, 1953), contributing to a mechanistic view of animals (Shepherdson 1998). Investigations often compared, for example, learning abilities between animals (usually rodents) raised in "enriched" versus "impoverished" environments (for a review, see Uphouse 1980). One of the consequences of this approach was the development of behavioural disturbances and even bizarre behaviours in the experimental animals used (e.g., Skinner 1948; see also Erwin et al. 1979; Novak et al. 2006). They sometimes could be "treated" by providing a richer spectrum of environmental or social stimuli (e.g., Harlow 1958). In the context of a behaviouristic approach, the (study) animals are likely to be predominantly regarded in the context of their reduced environment. Solutions to behavioural problems would be searched for by investigating potential discrepancies between the captive environment and the internal status of animals. Stimuli that are missing would be added (enrichment) (e.g., Harlow and Harlow 1962; Widman et al. 1992). A number of environmental enrichment and welfare studies and training programmes in zoos are based on this approach (for a review, see Fernandez and Martin 2021). Markowitz and his colleagues were among the first to use operant conditioning methods to "teach" animals (e.g., white-handed gibbons *Hylobates lar*) in zoos, for example, to procure food from a range of devices (e.g., Markowitz 1979, 1982). Through the "behavioural engineering" approach used in applied behavioural analysis (see Forthman and Ogden 1992), environmental components were "engineered" to create desired behavioural changes in zoo animals. As Markowitz and Aday (1998) elaborate, enrichment techniques in zoos were historically developed as band-aid solutions to compensate for poor living conditions in traditionally sterile and impoverished enclosures; and were meant to provide animals with some control over their environment. Hutchins et al. (1978a, b, 1979) criticised the behavioural engineering approach as simplistic and questioned the naturalness of the behaviours stimulated by the devices. Hancocks (1980) and Hutchins et al. (1984) proposed a "naturalistic approach" for designing enclosures that regards the animal predominantly in the context of its natural environment. In principle, captive conditions/keeping systems should be designed based on the knowledge of the biology of the species (and knowledge about the individuals involved). Captive conditions should allow the realisation of species-typical behaviour. This approach comes close to Hediger's concepts and seems to realise optimally "animal welfare" considerations. Living conditions of animals in their natural habitat, however, usually cannot perfectly be copied in a zoo. Naturalistic approaches, therefore, also may have to consider whether the "naturalistic" conditions offered in a zoo really meet the animals' needs. Forthman-Quick (1984) provide a review of both schools of thought and suggest an integration, while Mellen and MacPhee (2001) propose a "holistic approach" for a self-sustaining enrichment programme.

Animal welfare and enrichment studies and projects often claim that their (positive) effects might provide means to reduce breeding and sustainability problems. Currently, the latter have to be regarded as an important topic of zoo biology and population management.

Sustainability problems

Since the introduction of the "population paradigm" in the early 1980s, zoos have succeeded in supporting the persistence of a number of populations of threatened species of wild animals under human care (Hoffmann et al. 2010; Conde et al. 2011a, b; Bolam et al. 2021). However, many of the managed captive mammal and bird populations of threatened species have a low probability for long-term survival (Lees and Wilcken 2009; Leus et al. 2011a; Long et al. 2011). The populations are not sustainable due to low numbers of individuals, low levels of genetic diversity, and in particular poor reproduction (Barlow and Hibbard 2005; Baker 2007; Kaumanns et al. 2008; Stanley Price and Fa 2007; Lees and Wilcken 2009; Leus et al. 2011a; Long et al. 2011; Lacy 2013; Che-Castaldo et al. 2019). An overview of the current poor status of the North American captive populations is provided in a special issue of the journal *"Zoo Biology"* (volume 38, issue 1); an overview is provided by Powell et al. (2019).

Zoo biologists mainly discuss the sustainability problems as a consequence of small population sizes and deficits in demographic and genetic structures (e.g., Leus et al. 2011b) and derive potential solutions from the small population paradigm (e.g., metapopulation). Efforts to address the current sustainability crisis in AZA, for example, focus on developing new analytical tools to analyse large datasets and define the roles of species and goals of their respective population programmes (Powell et al. 2019). Discussions sometimes include attempts "to redefine "sustainability" by accepting lower viability indicator goals to improve the perception of programme "success"" (Putnam et al. 2022, p.4). Inter-regional or global meta-population management, derived from the work on a few successfully managed populations of, for example, golden lion tamarins (Ballou et al. 2002), and red pandas *Ailurus fulgens* (Glatston and Leus 2005), has been propagated in the last decade (Lees and Wilcken 2009; Leus et al. 2011a; Conway, 2011; Conde et al. 2013). The management of several small (national and regional) captive and possibly wild populations of threatened species under an integrated *in situ – ex situ* species conservation programme such as the "One-Plan" approach is proposed by the IUCN (SSC) Conservation Planning Specialist Group (Byers et al. 2013). Although coordination among zoos and other institutions on a global level is difficult (Conde et al. 2013) and some previous attempts were unsuccessful (Lees and Wilcken 2009), a few threatened species (one bird, eight mammals) are currently managed by the WAZA under a Global Species Management Plan (GSMP) (WAZA 2022). A small number of species that are managed in integrated *in situ – ex situ* projects under the "One-Plan" approach include Tasmanian devil *Sarcophilus harrisii*, northern bald ibis *Geronticus eremita*, and Andean condor *Vultur gryphus*, among others (Gilbert and Soorae 2017). Overall, however, most captive zoo populations of threatened species have a low potential for long-term sustainability (e.g., Che-Castaldo et al. 2019) and their contribution, for instance, to reintroductions and improving the status of wild populations has been limited (Griffith et al. 1989; Beck et al. 1994; Balmford et al. 2011; Brichieri-Colombi et al. 2019). For the lion-tailed macaque, a global conservation breeding programme with a core of European and Indian subpopulations in zoos is proposed. It should have a future prospect of conservation activities in its country of origin, India (**Chapter 4**).

The approaches and tools that are currently developed and propagated might help to cope with sustainability problems in some populations. The overall validity of the approaches has, however, been questioned by Kaumanns and Singh (2015) with reference to the currently used "small management paradigm" (see above) both for theoretical reasons and regarding the status of many captive populations (see also **Chapter 5**). They emphasise the necessity to assess the appropriateness of the globally standardised gene-biased management approach. Moreover, studies have indicated that sustainability problems emerge in many ways as a consequence of breeding problems (e.g., Penfold et al. 2014). The metapopulation approach by itself may not solve the underlying breeding problems. The problems emerging under the current management paradigm are not predominantly discussed as a consequence of individual breeding problems resulting from altered living conditions. Some studies have investigated the causes of low reproductive output in captive populations of, for instance, the African elephant *Loxodonta africana* and Asian elephant *Elephas maximus* (Brown et al. 2004, 2016; Hermes et al. 2004; Hildebrandt et al. 2006), white rhinoceros *Ceratotherium simum* (Hermes et al. 2006; Swaisgood et al. 2006), eastern black rhinoceros *Diceros bicornis michaeli* (Edwards et al. 2015), cheetah *Acinonyx jubatus* (Wachter et al. 2011; Ludwig et al. 2019), tiger *Panthera tigris* (Saunders et al. 2014), African lion *Panthera leo* (Daigle et al. 2015), and red panda *Ailurus fulgens* (Princée and Glatston 2016). An analysis by Penfold et al. (2014) on multiple captive populations revealed that management-induced non-breeding situations for extended time periods could lead to problems in the female reproductive system. The studies mentioned above identified several possible causes for the breeding problems, and in most of them, the authors point to the need to investigate behavioural aspects in the context of reproduction. It is likely that individuals in declining captive populations suffer from inappropriate breeding conditions. There might be mismatches between species-typical adaptations, living conditions in zoos, and management programmes.

Contributions of life-history theory

Life-history theory (Stearns 1976, 1977, 1992, 2000; Ricklefs 1991; Ricklefs and Wikelski 2002) emphasises that behaviour is a component of the individual phenotype itself, and the individual as a whole (with all its structural levels) is the unit of selection. Kaumanns and Singh (2015) provide a conceptual framework to consider the individual phenotype with its behaviour and life-history as the unit of management for captive propagation. They propagate that captive population management should be based on the concepts of evolutionary biology (see also Schulte-Hostedde and Mastromonaco 2015) with special emphasis on life- history theory. However, an analysis of a population with reference to aspects of the life-history of animals, including behaviour, requires long-term data on the life-history of individually recognisable animals. Long-term demographic data on individually known animals of many cooperatively managed captive populations is available in international and regional studbooks. The analyses of such studbook data are usually carried out using zoo-based software and include population-level measures such as population size and composition, birth rates, and measures of genetic constitution and relatedness. These parameters allow an analysis of the dynamics of the populations and a basis for further investigations of various aspects. Clutton-Brock and Sheldon (2010) elaborate on the importance of long-term studies that monitor the life histories of individually recognisable animals. They can provide insights into individual variation in breeding success and survival. Such analyses alone, however, do not allow the identification of proximate causes of change in population size. The present study uses a long-term dataset (*sensu* Clutton-Brock and Sheldon 2010). The study represents an approach to analyse captive populations that considers the role of individuals for the populations' productivity and long-term survival.

Study species: Lion-tailed macaque *Macaca silenus*

The lion-tailed macaque is one of the oldest (Delson 1980) of the *c.*22 macaque species (see Anandam et al. 2013). It belongs to the *Macaca silenus* group of the seven species groups of macaques as proposed recently (Zinner et al. 2013) and is possibly the closest descendant of the progenitor of all extant Asian macaques (Fooden 1975, 1980; Delson 1980; Abegg and Thierry 2002). It is considered the earliest and longest resident of the tropical rainforests of the Western Ghats of southern India (see Kumar 1987). Ram et al. (2015) suggested that the lion-tailed macaque underwent an ancient divergence *c.*2.11 million years ago into two distinct populations across the north and south of the Palghat gap that divides the Western Ghats into northern and southern regions. The individuals of the subpopulations do not differ in their outer appearance.

The lion-tailed macaque is a canopy dweller (Kurup and Kumar 1993; Singh et al. 2002), a habitat specialist (Singh et al. 1997), and is predominantly frugivorous (Sushma and Singh 2006). About 70–80% of its diet comprises fruits; animal matter, especially insects, comprises 14–18%, and the balance constitutes seeds and flowers (see Kumar 1987, Umapathy and Kumar 2000; Sushma and Singh 2006; Singh 2019). *Ficus* and *Cullenia exarillata* trees are important and predictable sources of food, specifically during periods of fruit scarcity (Krishnamani and Kumar 2018). They are regarded as keystone species for the macaques in the northern and southern regions of Western Ghats, respectively (Kumar et al. 1995a; Krishnamani and Kumar 2018). As the availability of fruits throughout the year and the high diversity of trees are likely only in evergreen rainforests, the lion-tailed macaque has always been confined to the rainforests (see Kumar 1985). Due to the limited and scattered distribution of food resources, the selective feeding on >200 food plants, and the need to assess the ripeness of fruits, and food processing, a considerable amount of their time is spent searching and foraging for food (Singh et al. 2001; Sushma and Singh 2006; Krishnadas et al. 2011; Krishnamani and Kumar 2018). They typically move through the canopy, foraging individualistically (Sushma and Singh 2006) while maintaining large inter-individual distances (Jeyraj 2003). The complex networks of canopies and important food trees for the macaques are, however, significantly reduced in most forest fragments (see Kumara et al. 2011) that suffered logging and other human-induced alterations (see above). Lion-tailed macaques in one such small, privately owned fragment (Puthuthotam estate in Valparai, studied since decades) seem to cope with these altered conditions via behavioural modifications to a largely terrestrial life and changes in their diet

(Singh et al. 2001; Dhawale et al. 2020). They now consume fruits and plant parts of many non-native and pioneer plants, including coffee seeds, as well as cultivated fruits such as bananas, and show an increased consumption of faunal food (Singh et al. 2001). The loss of canopy contiguity and fruit trees, unpredictable supply of non-native plants, dependence on trees also used by humans and long periods of time spent on the ground, roads, and residential areas, have kept the lion-tailed macaques in these areas under increasing pressure (Singh et al. 2001). Recent observations point to even more frequent use of, for example, garbage and food thrown by humans (see Jeganathan et al. 2018a). Road kills occur more frequently (Jeganathan et al. 2018b). There are efforts to reduce them by re-establishing canopy contiguity across roads via aerial bridges (Umapathy et al. 2011; Singh 2019).

Like foraging and movement, the social and reproductive systems of the lion-tailed macaque are adapted to its environment of limited food resources, which is subject to seasonal variations (see Kumar 1987). In the wild, the species breeds throughout the year (Krishna et al. 2006) but with a significant peak in births during January–April and a smaller peak during September–December (Sharma et al. 2006), indicating partial seasonality. Weaning takes place during the second year only. Fruit abundance, during monsoons only, is considered a limiting factor in their patterns of reproduction (see Sharma et al. 2006; Singh et al. 2006a) and possibly accounts for the species' long interbirth interval (see Singh and Kaumanns 2005). A further impediment to their reproduction is that a large part of the lion-tailed macaque population inhabits degraded forest fragments where food quality is poor. According to Kumar (1987) and Singh et al. (2006a), the species' life-history traits, such as a delayed age at first birth (*c.*6.5 years), low female lifetime reproductive output (*c.* five infants) but high infant survivorship (0.80–0.973), and long inter-birth intervals (30–36 months) (Kumar 1995; Singh et al. 2001, 2006a, 2009; Sharma 2002; Krishna et al. 2006), evolved as an adaptation to its rainforest environment. Due to these traits and a lack of abundant food resources, the population turnover has always been lower than that known for other macaques (Kumar 1987; Singh et al. 2000, 2006a). Kumar et al. (1995a) found that lion-tailed macaques had lower birth rates in forest fragments than in more contiguous habitats. Krishna et al. (2006) observed that in a forest fragment where the macaques were adapted to feed on fruits of exotic trees, the birth and survivorship rates did not decline. The quality of the resources in a habitat seems to be of critical importance (Kumar et al. 1995a). A management recommendation addressing this issue includes planting good shade trees for farmer's crops that can also serve as food trees for the macaques so that the reproductive output does not decline (Singh et al. 2006a).

Lion-tailed macaques, like other macaque societies, live in permanent, female-bonded social groups, where females remain in their natal groups throughout their lives and males are the dispersing sex (see Kumar 1987; Thierry et al. 2004). They tend to have a modal group size of 16–21 individuals in large contiguous forests (for example, Kumar 1987; Ramachandran and Joseph 2000; Kumara and Singh 2004b; Kumara et al. 2014; Sushma et al. 2014; Singh 2019). Group sizes are more variable in forest fragments ranging between 7 and 90 individuals (Singh et al. 2002; Umapathy and Kumar 2000; Umapathy et al. 2011). Typically, groups have a one male–multifemale social organisation, i.e., one adult male, subadult males, several adult females, juveniles, and infants (see Kumar 1987). The occurrence of several group members of different age-sex classes (and generations) allows conditions for socialisation and learning, including play among infants and juveniles (see Kaumanns et al. 2006; Singh et al. 2001). Members of groups that were isolated and remained small for long periods of time might lack the opportunities to develop the complete range of behaviours and social skills (see Singh and Kaumanns 2005). Females in a group have permanent relationships and strong bonds with related females (see Kumar 1987; Thierry et al. 2004). Groups are constituted by matrilines that coexist and remain stable for generations, and most interactions occur within matrilines (see Thierry et al. 2004; Singh et al. 2006b). Males, on the other hand, usually stay distant from each other and social interactions are rare (Singh et al. 2010). Males become peripheral at subadult ages and usually migrate between groups (Kumar 1987). In isolated and fragmented habitats, where inter-group male migration is almost absent, groups may have more than one adult male at a time (for example, Singh et al. 2002). Solitary males have been observed in rainforests. Inter-group encounters are common in overlapping home ranges and provide conditions that may precede the joining of new males in groups (see Kumar and Kurup 1985a) and the possibility of female choice. Adult females appear to prefer a new male to the resident adult male in all social interactions, including mating (Kumar et al. 2001). Key features of the species reproductive system include the formation of a consort relationship between a female in oestrous and a male (Kumar and Kurup 1985b; Kumar 1987); mating following a multiple-mount-to-ejaculate pattern (Fooden 1980; Lindburg et al. 1985; Sharma 2002), and severe reproductive competition among females (Kumar 1987). Harassment of mating partners by other female members is common and may disrupt mating and hinder fertilisation (see Kumar and Kurup 1985b; Kumar 1987; Kumar 2000; Sharma 2002). To avoid the latter, a consort pair moves away from the core group for extended periods (see Kumar and Kurup 1985b; Kumar 1987), which might be difficult for large groups inhabiting small fragments (see Singh and Kaumanns 2005). Small, isolated groups may fail to reproduce at all in case the only existing adult male dies or suffers from a breeding problem.

Population management recommendations suggested in this context have been: 1) the connection of neighbouring fragments with fruit trees that will allow male migration between isolated groups (Singh et al. 2001; Umapathy et al. 2011; Kumara et al. 2014), and 2) the management of group size and composition to allow appropriate socialisation and reproductive behaviour (Singh and Kaumanns 2005).

Study population: Global captive population of the lion-tailed macaque (*Macaca silenus*)

The captive population of the lion-tailed macaque exists since more than 100 years and has been systematically managed via regional breeding programmes (SSP, EEP) since the 1980s (Singh et al. 2009; Kaumanns et al. 2013). The breeding programmes were intended to establish a reserve population to support the wild population and its conservation (see Heltne 1985). The population underwent different periods and “types” of management, ranging from “no systematic management” to different types of systematic management carried out in the two main subpopulations (SSP, EEP). The global historical captive population consisted of over 2,700 individuals, including a living population of about 516 individuals. Its “International Studbook” provides long-term data sets on the population’s development and demography. The lion-tailed macaque, furthermore, has been comparatively well studied in the wild, thus providing reference data from field studies.

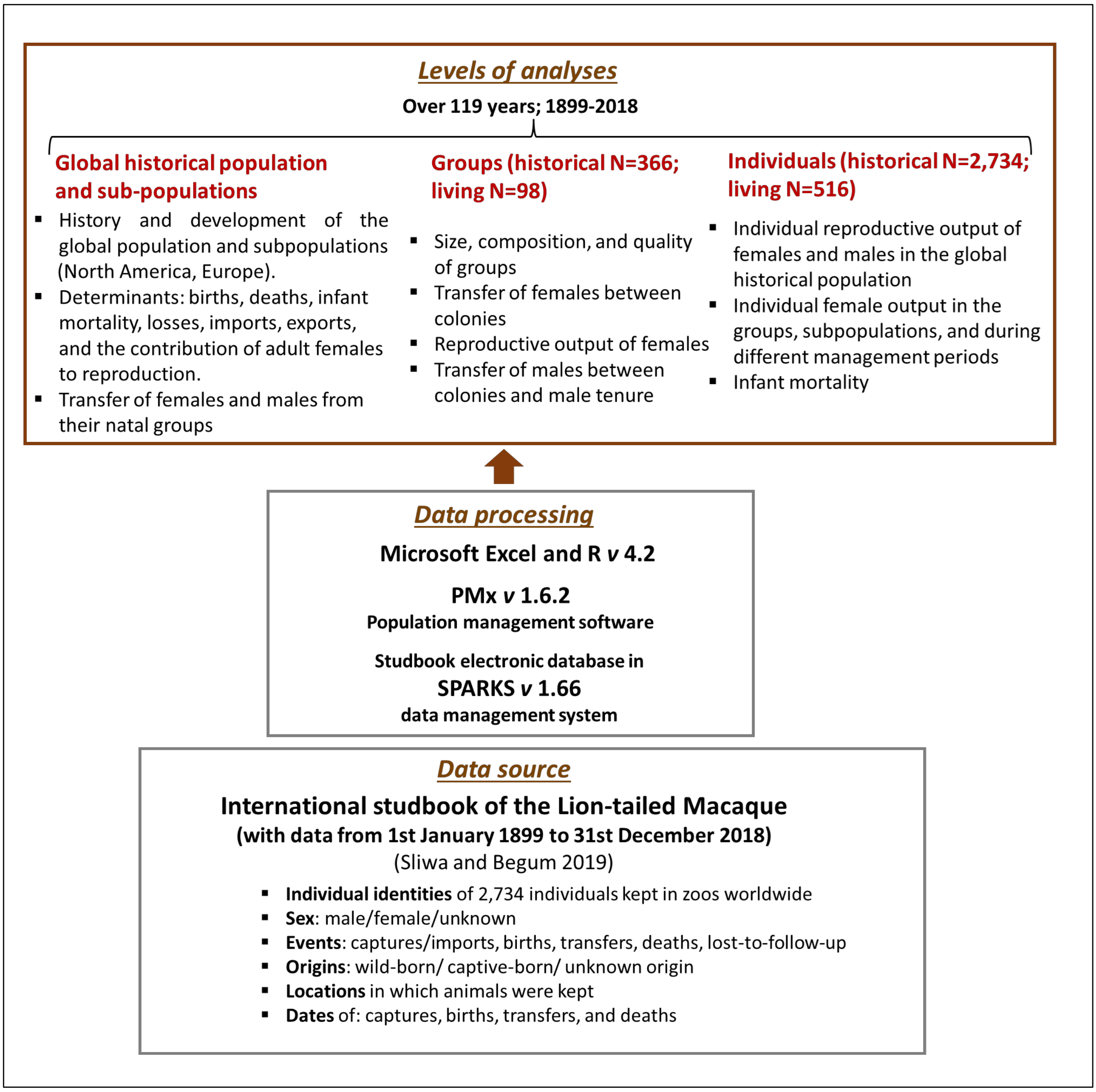
The captive population of the lion-tailed macaque is assumed to be one of the more successful captive primate populations. However, studies on the various subpopulations have hinted at breeding problems and possibly a low potential for long-term survival (Lindburg et al. 1989; Lindburg and Forney 1992; Lindburg 2001; Kaumanns and Rohrhuber 1995; Krishnakumar and Manimozhi 2000; Kaumanns et al. 2001, 2006, 2008, 2013; Singh et al. 2009). Consequently, the reproductive system has been in focus, and in particular, studies on physiological and behavioural aspects have been carried out. A number of these studies contributed significantly to the knowledge about the reproductive biology of the species (e.g., Shideler et al. 1983; Lasley et al. 1985; Lindburg et al. 1985; Lindburg 1990; Clarke et al. 1992; Harvey and Lindburg 2001; Heistermann et al. 2001; for a review, see Singh et al. 2006a). However, they were not followed up later and were not fully integrated into the breeding programmes. They were not sufficiently considered as part of a more complex aspect of the biology of the species. In particular, the role of the demography and social life as a milieu in which reproduction takes place was underestimated. Increased knowledge about the reproductive system was not used to establish an overall more productive population. Both large subpopulations, however, revealed periods in which increased knowledge and *in situ – ex situ* components were propagated and used (see below). By means of this, the European breeding programme supported the persistence of its “own” and the global population after the (management-induced) loss of the North American population.

In this study, the aspects of demography and its implications for the realisation of the species-typical social system are in focus with reference to productivity at individual and population levels.

For the lion-tailed macaque, comprehensive demographic data are available, and both its status in the wild and captivity require conservation-oriented management. Its captive population is a good model to investigate these aspects.

Aims of the study

The study intends to describe and analyse the development of the global historical captive population of the lion-tailed macaque *Macaca silenus* and its patterns of reproduction. By concluding from the overall development and, in particular, the patterns of reproduction, the potential of the population for its long-term survival is assessed, also with reference to its potential function as a reserve for the wild population. The study is based on a revised version of the international studbook prepared by Alexander Sliwa (EEP Coordinator) and Nilofer Begum (see Sliwa and Begum 2019). Figure 1 provides an overview of the levels of analyses.



Levels of analyses

Over 119 years; 1899-2018

Global historical population and sub-populations

- History and development of the global population and subpopulations (North America, Europe).
- Determinants: births, deaths, infant mortality, losses, imports, exports, and the contribution of adult females to reproduction.
- Transfer of females and males from their natal groups

Groups (historical N=366; living N=98)

- Size, composition, and quality of groups
- Transfer of females between colonies
- Reproductive output of females
- Transfer of males between colonies and male tenure

Individuals (historical N=2,734; living N=516)

- Individual reproductive output of females and males in the global historical population
- Individual female output in the groups, subpopulations, and during different management periods
- Infant mortality

Data processing

Microsoft Excel and R *v* 4.2

PMx *v* 1.6.2
Population management software

Studbook electronic database in
SPARKS *v* 1.66
data management system

Data source

International studbook of the Lion-tailed Macaque
(with data from 1st January 1899 to 31st December 2018)
(Sliwa and Begum 2019)

- **Individual identities** of 2,734 individuals kept in zoos worldwide
- **Sex**: male/female/unknown
- **Events**: captures/imports, births, transfers, deaths, lost-to-follow-up
- **Origins**: wild-born/ captive-born/ unknown origin
- **Locations** in which animals were kept
- **Dates** of: captures, births, transfers, and deaths

Figure 1. Overview of the levels of analyses for the study

The first aim of the study is to describe and analyse the full captive history of the lion-tailed macaque population and to identify important determinants of its development. It is asked whether its development and management contribute to achieving persistence and possibly to the conservation of the species in the wild. The study refers to different time periods and types of management the global population underwent.

The captive population of the lion-tailed macaque is regarded as a breeding device. The second aim of the study is to describe and analyse the patterns of reproduction with special emphasis on individual reproductive output. Analyses are carried out on various levels, including the global population, subpopulations, groups and across time periods (see Figure 1).

The productivity of the population was expected to be low. It is assumed that this is a consequence of mismatches between the altered living conditions in zoos and species-typical adaptations. It is intended to identify such mismatches. Alterations in living conditions are expected to be found with reference to the demographic and resulting social structures of the groups in which the individuals of the population were kept. We expect group sizes and demographic structures that reveal mismatches with species-typical groups in the wild. They may not allow the realisation of female-bonded structures typical for lion-tailed macaques and other macaque species. Information on the social units in which the individuals were kept, however, is not directly available from the studbook. The individuals kept in a location are therefore used as a proxy for groups. The identification of mismatches is unlikely to lead to a causal understanding of, for instance, breeding problems that have been reported since decades. The identification of mismatches, however, should facilitate the design of focused investigations on breeding problems. This can contribute to the development of appropriate global management approaches that consider the biology of the species. It might also provide hints on potential conservation issues in the fragmented wild population.

Overall, the analysis of the population should provide materials for the development of improved management programmes. It can also serve as a model for other species and provide materials for the management of the fragmented wild LTM population.

On a practical level, the results of the study are used to initiate the establishment of an international working unit that develops a programme for the management of the current global captive population towards more productivity and long-term persistence. An outline is integrated in the updated version of the international studbook and in a separate publication (see later).

Since many populations of wild animals in zoos, like the study species, lion-tailed macaque, are facing breeding and sustainability problems, aspects of the theoretical background of captive propagation and population management are analysed in a separate part of the study. It is believed that a change in basic management paradigms is required. An outline of a new paradigm is proposed.

Thesis outline

In **Chapter 2–Publication 1 (2022),** the history and development of the global captive population of the lion-tailed macaque are described and analysed. We investigate its determinants, such as births, deaths, infant mortality, imports, exports (immigration, emigration), and the contribution of adult females to reproduction. The analysis refers to different time periods, management policies, different subpopulations, and breeding programmes. The results are expected to provide information on the value of management approaches and the potential of the study population for long-term persistence as attempted by the breeding programmes. The study should also give hints on the species' potential to cope with altered environmental/living conditions as required for the conservation management of the wild lion-tailed macaques.

In **Chapter 3–Publication 2 (2023),** the study intends to look *behind* the overall development of the global historical captive population of the lion-tailed macaque in order to assess its potential for long-term persistence. It focuses on the investigation of the patterns of reproduction in terms of individual reproductive output and the distribution of group sizes over the full period of the existence of the global historical captive population. The investigation considers individuals, groups, regions, time, management periods, and selected aspects of the demography of the population, including the distribution of group sizes and the management-induced population dynamics via the transfer of individuals between groups. This study intends to identify alterations in living conditions that might establish mismatches with species-typical adaptations and potentially influence the productivity of the population. For the identification of mismatches, the following topics of the study are considered: 1) individual patterns of reproduction, 2) distribution of groups of different sizes, 3) transfers of females and males between zoo colonies, and 4) the fragmented nature of the population. It is intended to provide detailed descriptions of the results in the various parameters since they are supposed to provide reference data for population management, also for other primate species.

Chapter 4–Publication 3 (2021) mainly considers the conservation of the highly threatened lion-tailed macaque with reference to the potential contribution of the global captive population. It is especially addressed to professionals involved in decision-making and organising conservation activities. It intends to provide a short overview of the status and management history of the global historical captive population with special reference to the current population and its future management. Based on the new version of the international studbook (Sliwa and Begum 2019), selected results of the various analyses of the study population are provided, with a focus on the Indian captive population. From there, proposals for the future management of the current population are derived. They consider a special role of the Indian zoo community and conservation organisations within an *in situ – ex situ/* one-plan approach.

Chapter 5–Publication 4 (2020) is of a general nature and does not specifically refer to the study population. It rather deals with the viability and sustainability problems the management of captive populations of birds and mammals are confronted with. The investigations on the development and the patterns of reproduction of the study population also indicate corresponding problems. This paper elaborates on the conceptual background for, and the principles of, an improved management paradigm. The practical implementation of this general approach can vary between species and breeding programmes; therefore, the suggestions made in this paper remain on a general level. It elaborates why many captive populations face serious challenges and links their sustainability problems directly to the management of breeding problems. It provides a management approach that considers a captive population predominantly as a “breeding device”, the constituents of which, the individual members, are “designed for breeding”. The conceptual background is derived from concepts of evolutionary theory, in particular, the life-history theory. It is suggested to follow Caughley’s (1994) “declining population paradigm” contrary to the commonly practised “small population paradigm” with its strong emphasis on genetic aspects.

In **Chapter 6,** the main findings of the study are summarised and discussed with reference to the altered living conditions, resulting mismatches and potential limitations in terms of long-term persistence. The value and the limitations of the data, as provided by the international studbook (Sliwa and Begum 2019), are considered.

With reference to the methods, the International Studbook (Sliwa and Begum 2019) of the lion-tailed macaque provides the dataset used in this study coming from 366 zoo colonies. It covers the history of the captive population from 1899 to 2018. It contains all known records on the individual lion-tailed macaques as kept in zoos worldwide. Records comprise the individual identities, origins, sex, dates of births, transfers and deaths, locations, and parentage of captive-born animals. The current version of the studbook had to be newly established. Updated information about many of the zoo colonies as provided by the colony managers in the last decade since the publication of the previous edition of the studbook (2006) had to be integrated. Data for studbooks are provided by the zoos mainly via the web-based software ZIMS (Zoological Information Management System). The data had to be entered into the studbook programme SPARKS (Scobie and Bingaman Lackey 2012), checked for accuracy and validity, and prepared in organised formats for publication and use by zoo and population managers. The list of all individuals recorded historically (N = 2,734, ordered according to studbook numbers) and a list of all living individuals in zoos (N = 516, ordered per location) was completed. This list is essential for further management. In addition to the lists of individuals, a number of parameters like births, deaths, population development, current age-sex composition, and genetic status of the living population were analysed using the population management programme PMx (Ballou et al. 2022). The results were presented in the studbook. Furthermore, a report on the species biology based on recent literature was included. Since an international studbook is distributed worldwide to all current holders of the species and international zoo organisations, a preliminary version of **Chapter 4** was also presented there.

Chapter 2: Publication 1

A Hundred Years in Zoos: History and Development of the Captive Population of the Lion-tailed Macaque *Macaca silenus*. Long-term Persistence for Conservation?

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http://www.primate-sg.org/storage/pdf/PC36_Begum_et_al_100_years_captive_lion-tail_macaques.pdf

http://www.primate-sg.org/storage/pdf/PC36_Suppl_material_Begum_et_al_Lion-tail_macaque.pdf

Contributions of the authors

The conceptual framework and the manuscript of the study were developed by Nilofer Begum and Werner Kaumanns. Nilofer Begum carried out the organisation, and analysis of data and the visualisation of the results. Nilofer Begum, Werner Kaumanns, Mewa Singh, and Heribert Hofer contributed to the discussion of the results.

Primate Conservation 2022 (36): 155–172

A Hundred Years in Zoos: History and Development of the Captive Population of the Lion-tailed Macaque *Macaca silenus*. Long-term Persistence for Conservation?

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Abstract: Based on the recent international studbook, we here investigate the history and development of the global captive population of the Endangered lion-tailed macaque. Of particular interest is whether the development and management of the population has contributed to its persistence as a reserve population for the conservation of the species. Of the 2,734 individuals, 80% were born over 119 years. About 16% were wild-born and 4% were of unknown origin. The population was kept in two large differently managed subpopulations in North American and European zoos. It revealed a slow but steady increase from the 1960s onward with a period of 60 years of persistence till 2018 without imports of wild-caught individuals. The population grew under conditions of low productivity: only a small proportion of the females bred, and infant mortality was high. Overall, the number of births was slightly higher than the number of deaths. Reductions in population size and birth control measures due to space problems in both subpopulations led to a reduction of phenotypic diversity and a currently stagnating global population, mainly housed in European zoos. It still has the potential for developing toward a diversified and persistent population. The discussion suggests the need to: 1. Investigate the breeding problems; 2. Use adaptive management based on the "declining population" paradigm; 3. Consider the reproductive and social system as known from field studies; and 4. Emphasize international management structures especially with Indian zoos and conservation biologists.

Keywords: Lion-tailed macaque, endangered, global historical captive population, breeding programs, persistence, breeding problems, space, adaptive management

Introduction

Conservation Biology is a crisis discipline (Soulé 1985). The persistence of threatened animal populations under human-induced, altered living conditions is one of the main problems of conservation biology. Studies, for instance, focus on evolutionary consequences (Kinnison and Hairston 2007; Hendry *et al.* 2017) or the potential of the species to adapt, with special reference to behavioral responses to rapidly changing environments (Hendry *et al.* 2011; Tuomainen and Candolin 2011; Candolin and Wong 2012). Studies focusing on the behavioral adaptations or flexibility of primates in response to human-induced environmental changes contribute to our understanding of primate adaptive potentials and can be useful to optimize conservation efforts (Nowak and Lee 2013; Hockings *et al.* 2015; Strier 2017).

The lion-tailed macaque (*Macaca silenus*), a species endemic to the rain forests of the Western Ghats, southern India (for information on its biology, see Kumar 1987) is living under human-induced altered conditions. Its range and population structure are severely affected by habitat fragmentation and deterioration (Kumara and Sinha 2009; Singh *et al.* 2009; Kumara *et al.* 2014; Singh *et al.* 2020). The species is classified as Endangered (Singh *et al.* 2020). There are only about 4,000 individuals left in 47 subpopulations (Molur *et al.* 2003); the range of occupancy is small (Molur *et al.* 2003), and several life-history traits result in a low reproductive turnover (Kumar 1987; Singh *et al.* 2006). The lion-tailed macaque is a habitat specialist and has selective feeding habits (Kumar 1987; Singh *et al.* 1997; Sushma and Singh 2006; Krishnadas *et al.* 2011). A number of studies on the fragmented lion-tailed macaque population point to coping problems (Kumar *et al.* 1995; Kumar *et al.* 2018; Dhawale et al. 2020) but also coping potential (Singh *et al.* 1998; 2001; Krishna *et al.* 2006). Studies in the Anamalai Hills have revealed significant differences in their demographic parameters when compared to those in contiguous forests (Singh *et al.* 1998; Umapathy and Kumar 2000; Singh *et al.* 2002; Umapathy *et al.* 2011; Kumara *et al.* 2014; Sushma *et al.* 2014), but we lack continuous, long-term studies covering different subpopulations and groups and their development in the wild (Mewa Singh pers. obs. August 2020). They would help to predict the future development of the populations and to organize conservation measures (see Lindenmayer *et al.* 2012; Reinke *et al.* 2019).

The survival of lion-tailed macaques in their natural habitat, like that of many other primate species, may depend on conservation management (Singh et al. 2009, 2012) which must be based on an understanding of their adaptive potential and "behavioral tools" for coping with environmental change (Singh and Kaumanns 2005; Singh *et al.* 2006).

Captive populations in zoos have to cope with altered living conditions. They can be considered as an extreme case of small and fragmented populations due to space limitations, highly dispersed distribution, and the resulting alterations in demography and social structure (Kaumanns *et al.* 2008; Mason *et al.* 2013). We consider the global captive population of the lion-tailed macaque under this perspective and as a potential reserve for the wild population. It can be used to learn about the conservation management of the species under both conditions. The captive population of the lion-tailed macaque is one of the oldest, most dispersed, and largest managed primate populations. It experienced a number of different management approaches. The lion- tailed macaque was one of the first species discussed for *in situ/ex situ* linkages and the establishment of a breeding program with the purpose of establishing a reserve population in zoos (see Heltne 1985; Begum *et al.* 2021). Its international studbook covers a period of more than a hundred years and about eight generations. Such a long time may, as Lindburg (2001) notes for the North American lion-tailed macaque population, implicate changes in attitudes and interests in management and husbandry and their effects on the captive endeavor. Although often suffering from a lack of quantitative data, an investigation of the long-term history of a population can provide information on developments and events that were unpredictable or unexpected at the time of planning a program and can help to improve further management (see Lindenmayer *et al.* 2012; see also Kappelhof and Weerman 2020 describing the development of the red panda European breeding program).

Induced by the critical status of both wild and captive populations of the lion-tailed macaque, a number of studies have been published on the latter's status and development, and on aspects of husbandry and management. Most articles have reported that the growth of the captive population was unsatisfactory due to breeding problems and high infant mortality (see, for instance, Heltne 1985; Lindburg 1980, 2001; Lindburg *et al.* 1989; Lindburg and Forney 1992; Kaumanns and Rohrhuber 1995; Kaumanns *et al.* 2008, 2013; Singh *et al.* 2009). These studies concern just parts of the global population and cover limited time periods. The present study investigates the long-term development of the entire global captive population of the lion-tailed macaque till 2018.

Besides tracing the full captive history of a threatened primate, our study aims to investigate whether the development and management of the historical global captive population of the lion-tailed macaque contributed to achieving persistence and the means to support the conservation of the species, and to the maintenance of a reserve population. It is based on the study by Kaumanns *et al.* (2013) that covered the period till 2007 and concentrated on the European and North American subpopulations. The study presented here includes an update of the further development of the global population following the use of population size and birth control measures in both of these large subpopulations that may have critically influenced the persistence of the global population. The next management steps may be decisive for the long-term persistence and the quality of the future global population. The study presented provides relevant materials for the development of appropriate global management.

We investigate the determinants of the development of the global historical captive population such as births, deaths, infant mortality, imports, and exports (immigration, emigration), and the contribution of adult females to reproduction. We analyze its development with reference to different time periods, management policies, different subpopulations, and breeding programs. The results are expected to provide information on the value of management approaches and the potential of the study population for long-term persistence as attempted by the breeding programs. The study should also give hints on the species' potential to cope with altered environmental/living conditions (see also Jeschke and Strayer 2006; Sih *et al.* 2011; Mason *et al.* 2013) as required for conservation management of the wild lion-tailed macaques. Due to the nature of the available data for our study—studbook records and information on aspects of the history and management of the population from earlier publications—our investigation will remain on a descriptive level and is not intended to test hypotheses. For the value of studbooks as sources of data see Princée (2016).

Our study, as a model, can contribute to an understanding of the sustainability problems as found in many animal species in zoos (for example, Lees and Wilcken 2009; Leus *et al.* 2011; Powell *et al.* 2019).

Animals and Methods

The study deals with the 2,734 lion-tailed macaques kept in zoos worldwide over a period of more than 100 years, in a total of 366 institutions. Evidently, the individuals of the study population had different backgrounds and lived under heterogeneous conditions. This may include group size and composition, duration of the breeding units (groups), timescale, enclosures, transfers to different zoos, management styles (local and regional), and husbandry practices. The individual members of the population and the social units were highly dispersed in space and time.

The main source of data is the most recent edition of the international studbook of the lion-tailed macaque (Sliwa and Begum 2019, updated from Fitch-Snyder 2006) covering the period from 1 January 1899 (first captive specimen was recorded) to 31 December 2018. A first comprehensive survey on the global captive population was carried out in the 1980s and resulted in the first edition of the international studbook (Gledhill 1987; also, Lindburg 1980).

The studbook is maintained as an electronic database in the global studbook program, Single Population Analysis and Records Keeping System, SPARKS v 1.66 (Scobie and Bingaman Lackey 2012). We analyzed the data with the population management program PMx v 1.6.2 (Ballou *et al.* 2020), available from the Species Conservation Toolkit Initiative (<https://scti.tools>). To prepare the data for further analyses, we transferred all information from PMx into Microsoft Excel. We refer to demographic parameters such as population size, births, deaths, imports (immigration), and exports (emigration).

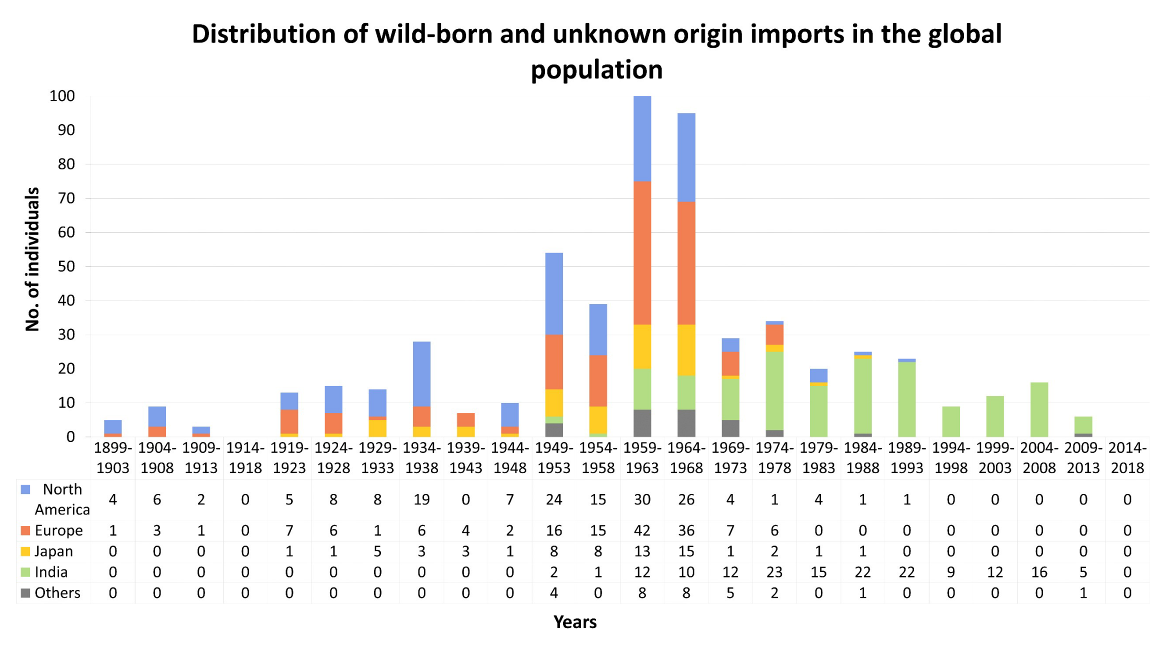
We analyzed the complete studbook population, comprising 2,734 lion-tailed macaques. Records had been noted by local institutional staff, and later pooled by regional studbook keepers. For most animals, information was available for birth dates, capture dates/estimates, birth type (wild-born/ captive-born/ unknown origin), sex, location, parentage of captive-born animals, dates of death and transfers between regions (see Sliwa and Begum 2019; Supplementary Materials). When the fates of individuals after birth/ capture and transfer could not be traced, they are referred to as lost-to-follow-up.

Information on management policies, population statuses, and other relevant aspects to describe aspects of the population development are taken from published studies and species reports of the North American (Species Survival Plan, SSP) and European (European Endangered Species Program, EEP) breeding programs.

Results

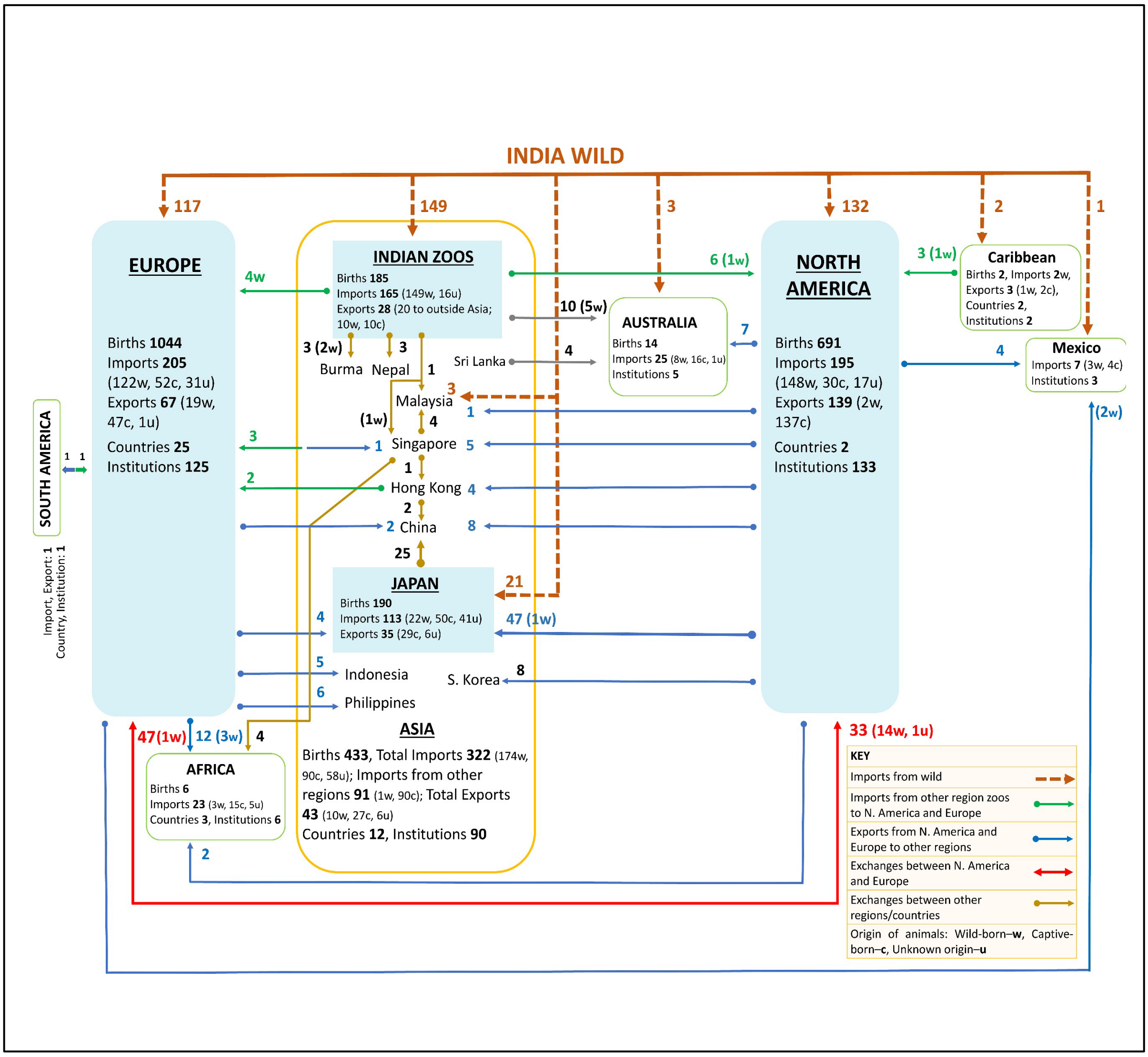
Origins

European and North American zoos started acquiring and keeping wild-born lion-tailed macaques in the late 19th and early 20th centuries for exhibition purposes. Figure 1 shows the distribution of wild-born and unknown origin individuals (probably also wild-born, see Lindburg and Forney 1992) in different regions over five-year intervals. The majority of the wild-born individuals were exported from India to North America (*c.*31%, n = 132) and Europe (*c.*27%, n = 117) (see Flowchart 1). They established subpopulations of similar size and composition. The majority of the exports were realized in the 1950s and 1960s. Thirty-five percent of the wild-born animals remained in Indian zoos. Only a few wild-born animals were exchanged between the regions (Flowchart 1).



	1899-1903	1904-1908	1909-1913	1914-1918	1919-1923	1924-1928	1929-1933	1934-1938	1939-1943	1944-1948	1949-1953	1954-1958	1959-1963	1964-1968	1969-1973	1974-1978	1979-1983	1984-1988	1989-1993	1994-1998	1999-2003	2004-2008	2009-2013	2014-2018
North America	4	6	2	0	5	8	8	19	0	7	24	15	30	26	4	1	4	1	1	0	0	0	0	0
Europe	1	3	1	0	7	6	1	6	4	2	16	15	42	36	7	6	0	0	0	0	0	0	0	0
Japan	0	0	0	0	1	1	5	3	3	1	8	8	13	15	1	2	1	1	0	0	0	0	0	0
India	0	0	0	0	0	0	0	0	0	0	2	1	12	10	12	23	15	22	22	9	12	16	5	0
Others	0	0	0	0	0	0	0	0	0	0	4	0	8	8	5	2	0	1	0	0	0	0	1	0

Figure 1. Distribution of wild-born and unknown origin imports in the regions over five-year intervals between 1899–2018. The data comprise 426 wild-born and 109 unknown origin animals with known import dates.



Flowchart 1. Transfers from the wild and between regions. The regions are indicated in the boxes: they include the total number of births, imports, exports, in the regions as well as the number of countries and institutions that housed captive lion-tailed macaques. The transfer of individuals from the wild in India to zoos worldwide and between regions are indicated by arrows. The number of individuals transferred are indicated above or beside the arrows. Most animals transferred between regions were captive-born but when they included wild-born or unknown origin individuals, they are indicated in parentheses near the arrows.

Origins and development

Figure 2 shows the contribution of wild-born, unknown origin, and captive-born individuals to the global population development. During the first *c.*70 years of the history of the population, most lion-tailed macaques in zoos were imported from the wild (Figs. 1 and 2; see also Flowchart 1). Only a few births occurred (n = 9) in the first 50 years. Most of the current population is derived from individuals caught between 1950 and 1970. Of the 428 wild-born individuals, 32% (n = 138; 56 males, 82 females) reproduced. The increase in population size from the mid-1970s onward was constituted by individuals born into the population. The increase was characterized by consistent fluctuations in the patterning of births (see Fig. 6.) throughout the years since *c.*1960 and overall, only slightly higher numbers of births than of deaths. The number of births and deaths per year between 1970 and 2018 averaged 41.3±12.71 (range 14–66) and 34.2±11.5 (range 8–58), respectively. The annual population growth rate (lambda, λ) during this time ranged from 0.954 (in 2015) to 1.08 (in 1973). A comparison of the mean lambda values per decade between 1950 and 2018 reveals a declining trend in the last decade (Flowchart 2).

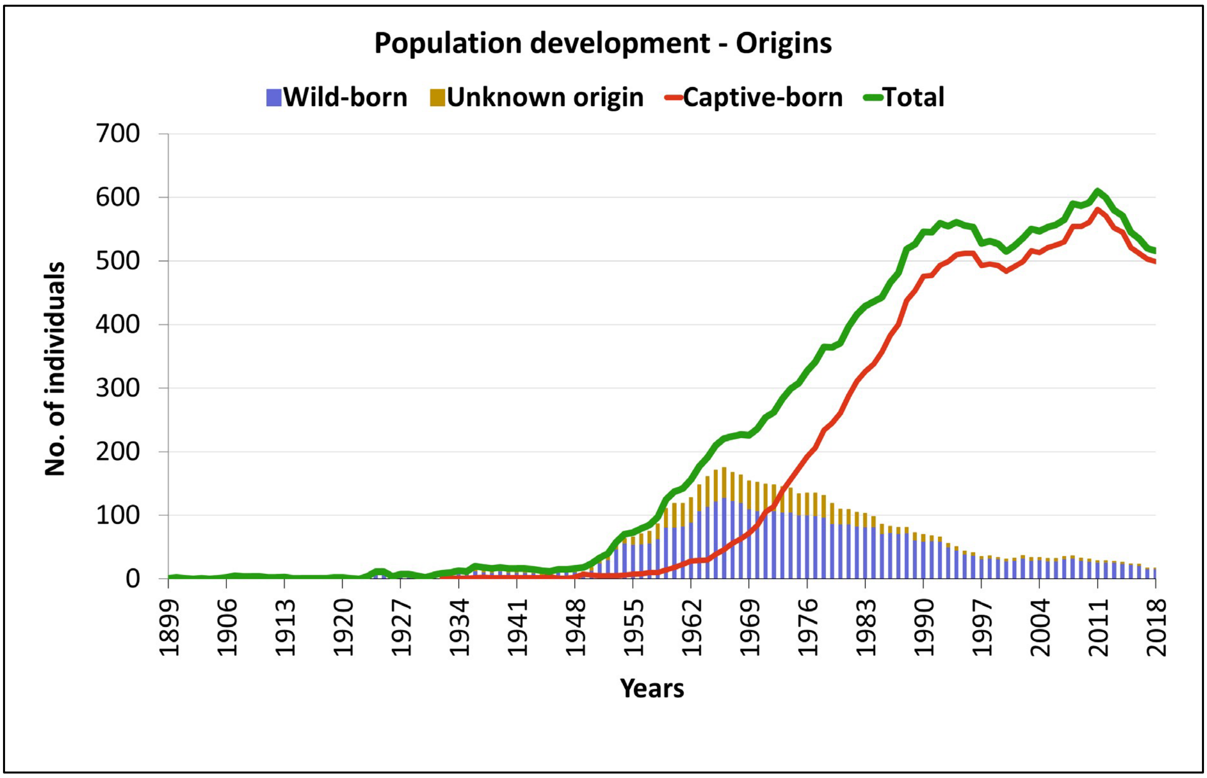


Figure 2. Global historical population and the origins.

The subpopulations

Figure 3 shows the major subpopulations constituting the global population with a dominant role of the North American and European subpopulations. It reveals a decrease in population size in both of the large subpopulations from 1988 (North America) and 2013 (Europe), onward, till 2018 (studbook period).

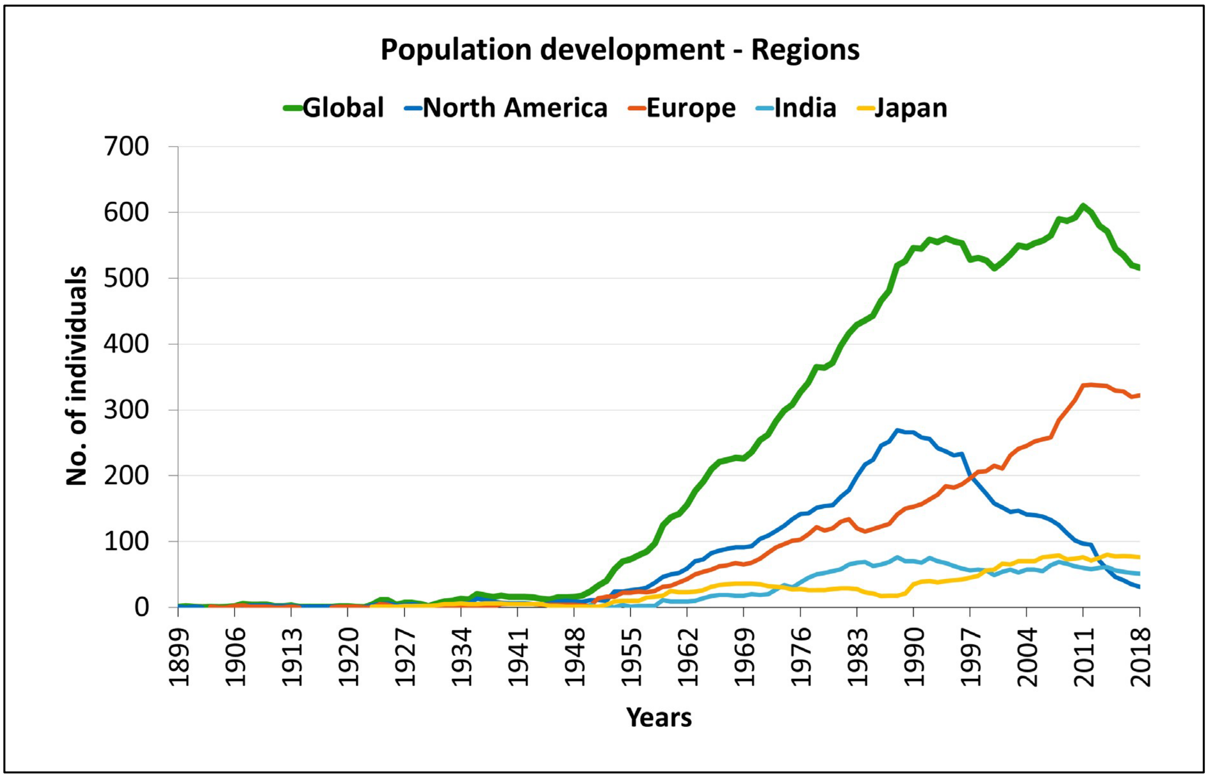


Figure 3. The major regional subpopulations of North America, Europe, Japan, and India within the global historical population during 1899–2018.

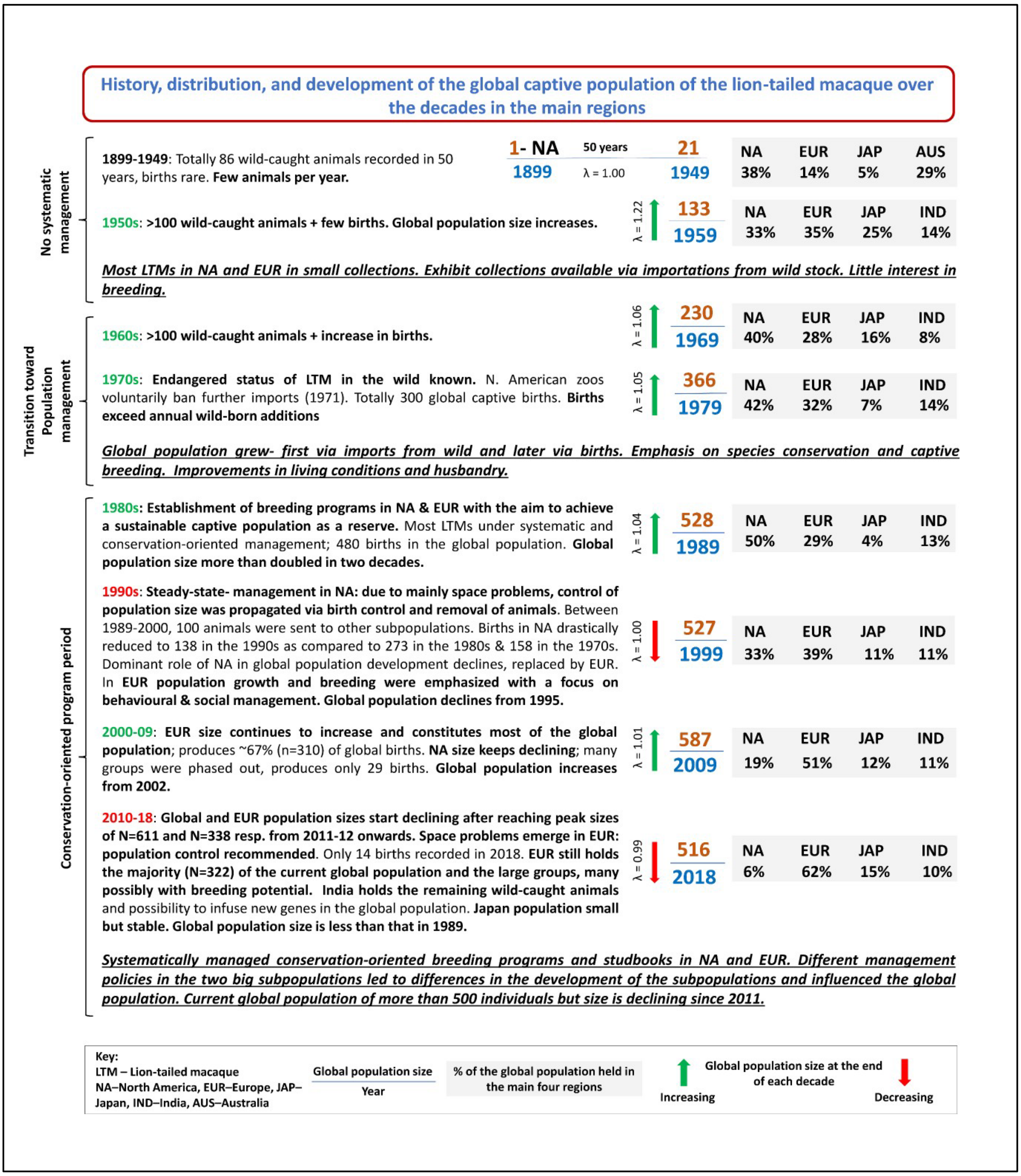
Transfers between regions

Flowchart 1 shows the patterning of transfers of lion-tailed macaques between the subpopulations and continents, respectively, and their contribution to the global population in terms of the number of births. The North American and European subpopulations with together 78% (n = 1707) of the births since the 1960s were developed and managed to a large extent independently (see flowcharts 1 and 2). North America and Europe exchanged 80 animals (15 wild-born, 64 captive-born, 1 unknown origin) between them, of which 74% (n = 59) were transferred in the 1980s and 1990s. Transfers from North America to Asia contributed to the establishment of some small peripheral populations. At present, India and Japan together constitute about 25% of the global population (Fig. 3, Flowchart 2).

History and distribution of the global population

The global historical population of the lion-tailed macaque was widely dispersed in time and geographically. Flowchart 2 provides an overview on its development with reference to its major subpopulations over various timeperiods and management styles. In the first decades, the breeding units of the population were managed locally (see Lindburg *et al.* 1989, 1997), followed by a transition period in which more breeding was propagated to preserve a stock of lion-tailed macaques in the zoos (Hill 1971; Lindburg and Harvey 1996). Regional and international management programs were initiated in the 1980s (Heltne 1985; Kaumanns and Rohrhuber 1995). The flowchart indicates differences in management style between the two big subpopulations and the use of birth control measures in both, at different times. For the European population, the natural growth of groups based on female bonds was recommended (Kaumanns *et al.* 2013). For the North American population, genetic management (Foose and Conway 1985) and control of population size toward a steady state were emphasized (Lindburg *et al.* 1997).

The flowchart shows that the North American subpopulation played a dominant role in terms of size and productivity till the 1990s; followed by a decrease that ends with a non-productive small population of about 30 individuals (see Lindburg 2001; Ness 2013; Sarno 2018). The dominant role was taken over by the European subpopulation that itself started to decrease from 2012 onward. The latter's decrease in size was due to a strong (management-induced) decrease in the number of births (see Sliwa *et al.* 2016). In 2018 it nevertheless still constitutes more than 60% of the living global population. The Japanese subpopulation remained stable in size over the last decade. The Indian subpopulation is shrinking with a low reproductive output (Begum *et al.* 2021) but it includes a number of wild-born, potential founders (Sliwa and Begum 2019). The current global population comprising 516 individuals is comparable to the population size in 1988 (n = 519), with, however, a changed subpopulation structure.



History, distribution, and development of the global captive population of the lion-tailed macaque over the decades in the main regions

1899-1949: Totally 86 wild-caught animals recorded in 50 years, births rare. **Few animals per year.**

1- NA 1899 — 50 years, λ = 1.00 — 21 1949

NA	EUR	JAP	AUS
38%	14%	5%	29%

1950s: >100 wild-caught animals + few births. Global population size increases.

λ = 1.22 — 133 1959

NA	EUR	JAP	IND
33%	35%	25%	14%

Most LTMs in NA and EUR in small collections. Exhibit collections available via importations from wild stock. Little interest in breeding.

1960s: >100 wild-caught animals + increase in births.

λ = 1.06 — 230 1969

NA	EUR	JAP	IND
40%	28%	16%	8%

1970s: **Endangered status of LTM in the wild known.** N. American zoos voluntarily ban further imports (1971). Totally 300 global captive births. **Births exceed annual wild-born additions**

λ = 1.05 — 366 1979

NA	EUR	JAP	IND
42%	32%	7%	14%

Global population grew- first via imports from wild and later via births. Emphasis on species conservation and captive breeding. Improvements in living conditions and husbandry.

1980s: Establishment of breeding programs in NA & EUR with the aim to achieve a sustainable captive population as a reserve. Most LTMs under systematic and conservation-oriented management; 480 births in the global population. **Global population size more than doubled in two decades.**

λ = 1.04 — 528 1989

NA	EUR	JAP	IND
50%	29%	4%	13%

1990s: Steady-state- management in NA: due to mainly space problems, control of population size was propagated via birth control and removal of animals. Between 1989-2000, 100 animals were sent to other subpopulations. Births in NA drastically reduced to 138 in the 1990s as compared to 273 in the 1980s & 158 in the 1970s. Dominant role of NA in global population development declines, replaced by EUR. In **EUR population growth and breeding were emphasized with a focus on behavioural & social management. Global population declines from 1995.**

λ = 1.00 — 527 1999

NA	EUR	JAP	IND
33%	39%	11%	11%

2000-09: EUR size continues to increase and constitutes most of the global population; produces ~67% (n=310) of global births. **NA size keeps declining**; many groups were phased out, produces only 29 births. **Global population increases from 2002.**

λ = 1.01 — 587 2009

NA	EUR	JAP	IND
19%	51%	12%	11%

2010-18: Global and EUR population sizes start declining after reaching peak sizes of N=611 and N=338 resp. from 2011-12 onwards. Space problems emerge in EUR: population control recommended. Only 14 births recorded in 2018. **EUR still holds the majority (N=322) of the current global population and the large groups, many possibly with breeding potential. India holds the remaining wild-caught animals** and possibility to infuse new genes in the global population. **Japan population small but stable. Global population size is less than that in 1989.**

λ = 0.99 — 516 2018

NA	EUR	JAP	IND
6%	62%	15%	10%

Systematically managed conservation-oriented breeding programs and studbooks in NA and EUR. Different management policies in the two big subpopulations led to differences in the development of the subpopulations and influenced the global population. Current global population of more than 500 individuals but size is declining since 2011.

Key:
LTM – Lion-tailed macaque
NA–North America, EUR–Europe, JAP–Japan, IND–India, AUS–Australia

Global population size / Year

% of the global population held in the main four regions

Global population size at the end of each decade
Increasing ↑ **Decreasing** ↓

Flowchart 2. A summary of the history, distribution, and development of the global population over the decades in the four main regions. Literature used: Hill (1971); Gledhill (1991); Lindburg and Forney (1992); Lindburg et al. (1997); Kaumanns et al. (2013); and Sliwa et al. (2016).

Determinants of population development and patterns of management

Of the 2,734 individuals, 80% (n = 2195) were born into the global historical population in 119 years. About 16% (n = 428) were wild-born, and 4% (n = 111) were of unknown origin. The deaths of 1,923 individuals were recorded; 295 animals were lost-to-follow-up. The determinants of the long-term development of the global population such as imports of wild-born and unknown origin animals, births, deaths, and losses per year are shown in Figure 4. Figures 5 and 6 show these parameters as well as imports of captive-born animals and exports for the North American and European subpopulations, respectively.

From 1970 to 1994, the number of births overall (n = 1050) was slightly higher than the number of deaths (n = 738) and the individuals that were lost-to-follow-up (n = 97), combined, which led to an increase in the size of the global population. The number of deaths (mainly influenced by infant mortality, see below) increased with population size both in the global population and in the subpopulations (Figs. 4, 5 and 6). After a decrease in the number of births and a decrease in the size of the global population during 1995–2000, both parameters increased overall again till 2011. A continuous decrease followed till 2018. The first decrease in the global population (1995–2000) was triggered by a management-induced decrease in the North American population. The second (2012–2018) was due to a management-induced decrease in population size in Europe (see Figs. 5 and 6.). The number of births recorded in 2018 (n = 14) was the lowest since 1966 (n = 16). Management in this decade aimed at low productivity.

A comparison of the patterns of population development in the two large subpopulations shows that the increase and decrease in population size and number of births overall were faster and steeper in the North American population. In North America and Europe, the annual number of births exceeded the addition of wild-born animals from 1966 and 1968, respectively, and the annual proportion of captive-born animals surpassed that of wild-born animals from 1971 and 1972, respectively.

In North America, from 1966 till 1988, the annual growth rates (λ, lambda) ranged between 1.006 and 1.118. Since 1989, the annual growth rate remained almost consistently <1; the mean value of lambda between 1989 and 2018 was 0.93. Sixty-five percent (n = 447) of all births in the region was recorded during 1966–1988. The number of births (n = 36) and population size (n = 269) in North America, peaked in 1987 and 1988, respectively. After this period, the number of births overall decreased due to birth control measures and due to the removal of more than 100 individuals. The number of housing institutions steadily decreased from, maximally, 36 in 1990 to 13 in 2018. The current population of 31 animals in 13 zoos (in 2018), is comparable to the situation in 1959 when 30 animals were held in 12 North American zoos.

In Europe, in a span of 45 years, 1968–2012, the annual growth rate (λ, lambda) ranged between 0.896 and 1.122. The number of births (n = 49) and population size (n = 338) peaked in 2008 and 2012, respectively. A slow decline in population size from 2012 was influenced by birth control measures and the export of a few individuals to other regions. The number of housing institutions increased and peaked in 2015 (n = 44) and has remained stable in the past years.

The decreases in population size as described above for the subpopulations, were due to "invasive management" procedures that, in the case of the North American population, finally led to a non-breeding status. Figure 5 shows that the decrease in the North American population started within a few years from the onset of the breeding program in 1983. In the European population, the onset of population control started more than twenty years after the establishment of the breeding program in 1989. This later onset of population control in Europe allowed the "occurrence" of 637 births during 1989–2011. In both the subpopulations, birth control measures were initiated when population size and the number of births peaked.

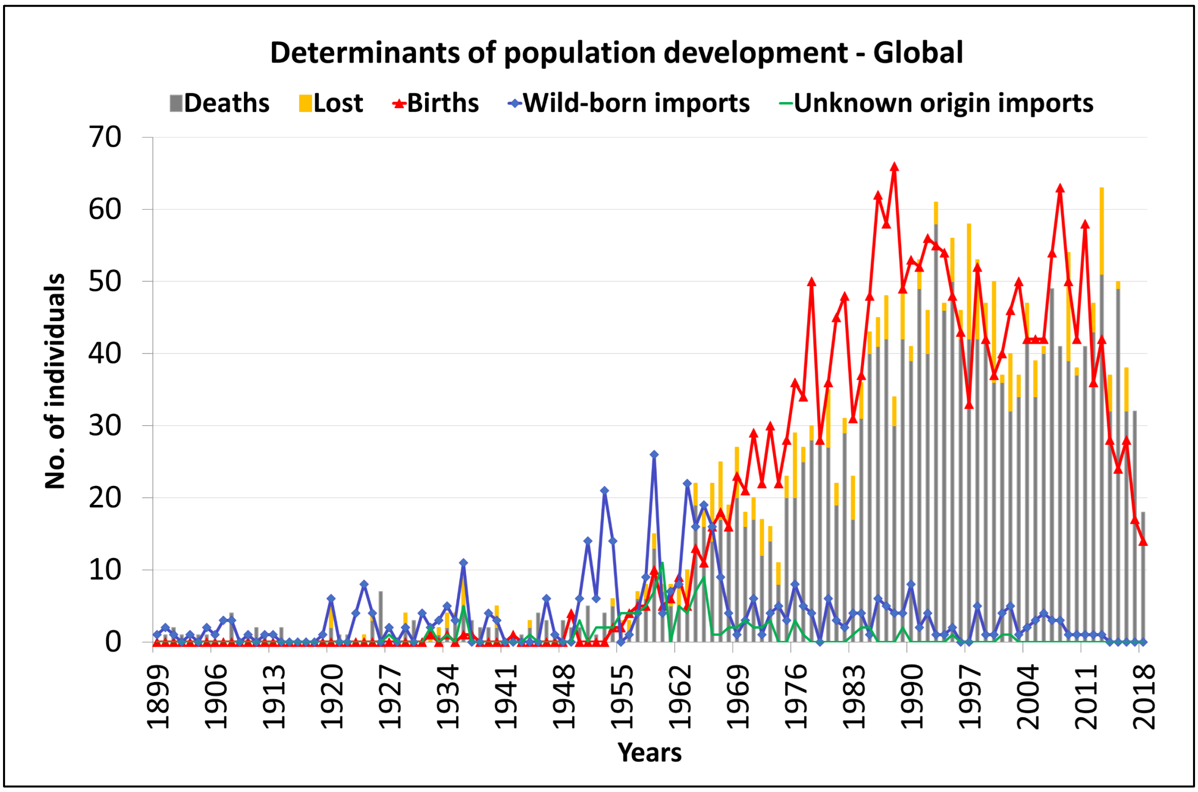


Figure 4. Determinants of population development – Global. Annual number of births, imports of wild-born, and unknown origin animals, deaths, and lost individuals (based on 426 wild-born, 2182 captive-born, 109 unknown origin, 1915 dead and 295 lost-to-follow-up individuals).

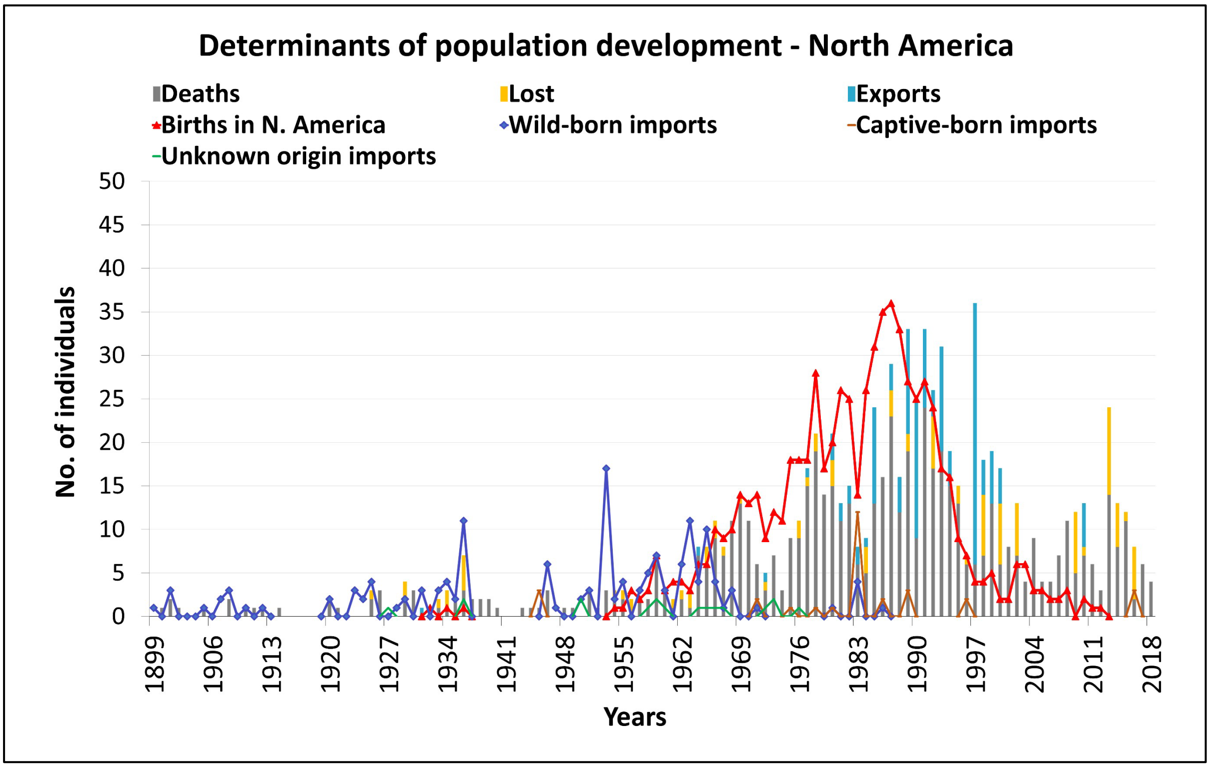


Figure 5. Determinants of population development – N. America. Annual number of births, imports of wild-born, captive-born, and unknown origin animals, deaths, exports, and lost-to- follow-up individuals.

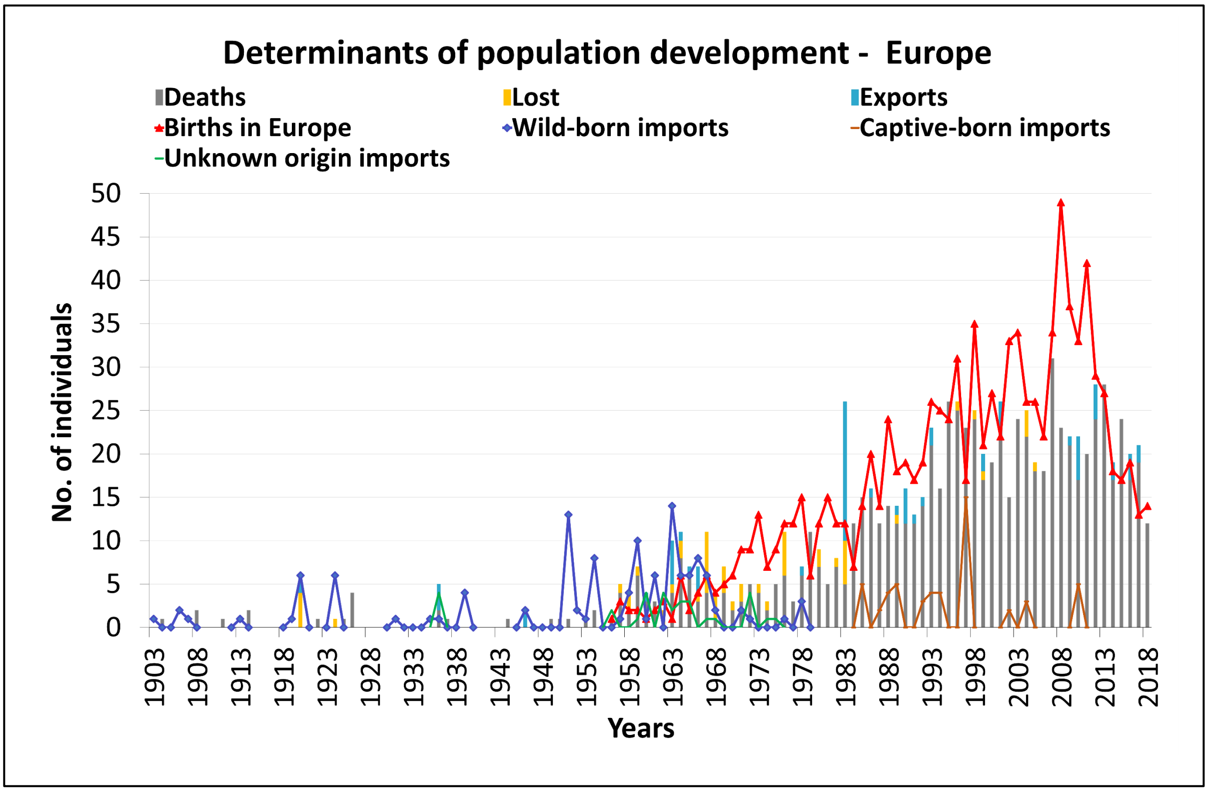
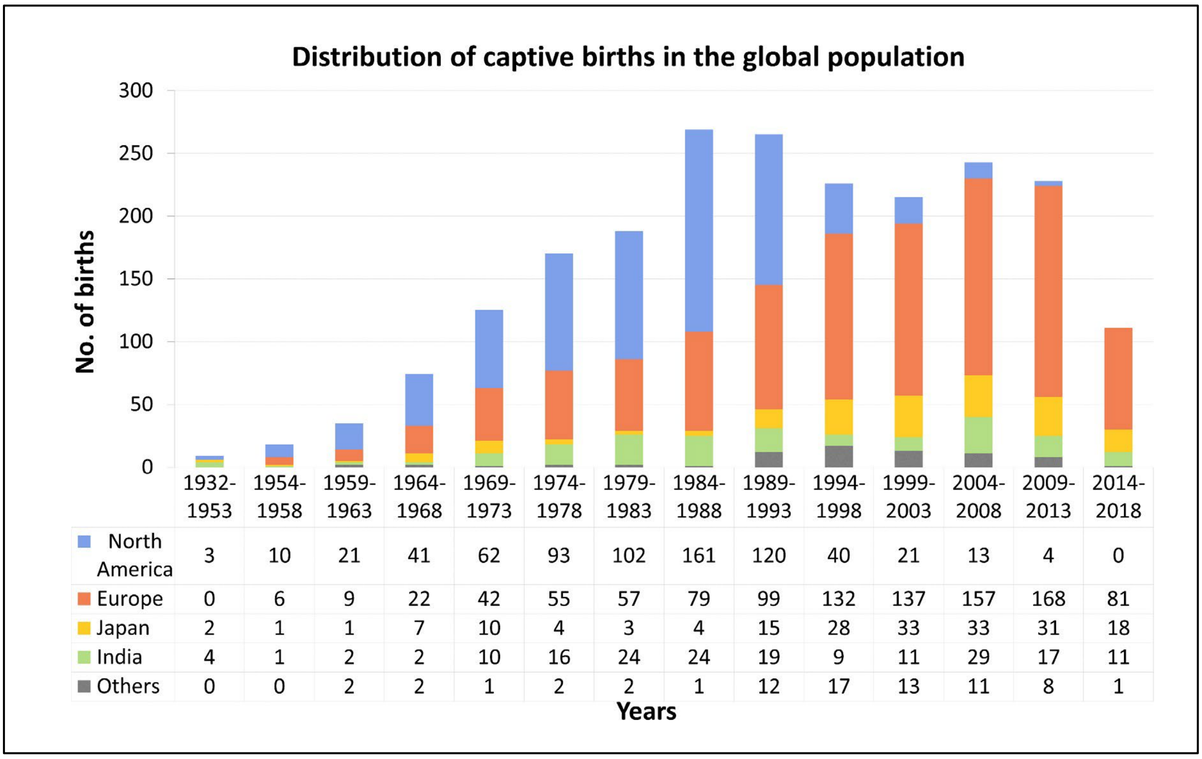


Figure 6. Determinants of population development – Europe. Annual number of births, imports of wild-born, captive-born, and unknown origin animals, deaths, exports, and lost-to-follow-up individuals.

Breeding, infant mortality, productivity

Contrary to earlier decades, from the 1960s onward breeding was explicitly propagated and increasingly realized until population control was introduced (Flowchart 2). Figure 7 shows the number of births per region in five-year intervals. It visualizes the "backbone" of population development. It demonstrates the importance of the North American population for early global population growth till about the mid-1990s and the change of importance toward the European population, and the smaller subpopulations, especially Japan and India. Population size and the number of births increased steadily over decades in the North American subpopulation prior to the establishment of a breeding program in 1983, and continued to increase for about another five years, after which both steadily decreased. The size of the European population and the number of births increased almost steadily since the establishment of the breeding program in 1989 till 2012.



	1932-1953	1954-1958	1959-1963	1964-1968	1969-1973	1974-1978	1979-1983	1984-1988	1989-1993	1994-1998	1999-2003	2004-2008	2009-2013	2014-2018
North America	3	10	21	41	62	93	102	161	120	40	21	13	4	0
Europe	0	6	9	22	42	55	57	79	99	132	137	157	168	81
Japan	2	1	1	7	10	4	3	4	15	28	33	33	31	18
India	4	1	2	2	10	16	24	24	19	9	11	29	17	11
Others	0	0	2	2	1	2	2	1	12	17	13	11	8	1

Figure 7. Distribution of captive births in the regions over five-year intervals from 1954 onward. Due to very few births between 1932–53, these are condensed in one category. The data used comprise 2182 births with known birth dates and known birth regions.

Up to 1993, the North American and European subpopulations revealed similar numbers of births (n = 332 in North America, n = 369 in Europe). Whereas the numbers in Europe increased almost steadily up to 2011, the numbers in the North American population decreased sharply toward zero between 2014 and 2018. Overall, since 2014, a trend toward a decrease in the number of births can be found in all the subpopulations. The overall decrease in productivity is reflected in the fact that the number of births in the years 2014–2018 is lower than that between 1969 and 1973.

Figure 8 refers to another important determinant of population development–infant mortality. Between 1964 and 2018, mean infant mortality per year was 30±11% (range 3–52%). Figure 8 shows that infant mortality was high overall. Thirty percent (n = 658) of the infants born in the global population did not survive to the age of 1 year (Fig. 9). In the subpopulations, 29% (n = 198) of the infants born in North America and 32% (n = 337) born in Europe, respectively, did not survive to one year. In both the subpopulations, most infant deaths occurred within the first 30 days of life, i.e., 24% (n = 164) and 27% (n = 285) of all the infants born in North America and Europe, respectively, failed to survive 30 days.

Of the total 2,182 individuals born into the population (known birth dates), 30% died earlier than one year of age (n = 658); 25% within the first month of life (n = 550). These deaths under 1 year represent 44% of the 1,495 captive-born individuals that died. About 42% of the 2,182 infants born, died (n = 837) or were lost-to-follow-up (n = 85) before the age of five years. Overall, therefore, more than 40% of the captive-born individuals of the population were not available for breeding.

In total, only about 63% (n = 500) of the females that reached adulthood (n = 800) bred at all, comprising 40% of all females recorded in the studbook (n = 1246). The proportions were similar in both the big subpopulations. About 40% (n = 156) and 41% (n = 240) of the total females recorded in North America (n = 395) and Europe (n = 588), respectively, gave birth at least once. The proportion of breeding males was even lower, as ongoing analysis reveals. Figure 10 provides information on the proportion of adult females in the global population that bred per year. It allows a rough assessment of the productivity of the population. Since 1954, when regular breeding was recorded, a mean of 27±9% (median 28%; range 8–49%) of adult females bred per year. Whereas the number of adult females in the population increased continuously till 1995 and again during 2011–2018, the breeding part of the adult female population since 1989 was only occasionally >35%. Productivity appears to be low, especially under conditions of high infant mortality (see Fig. 8.).

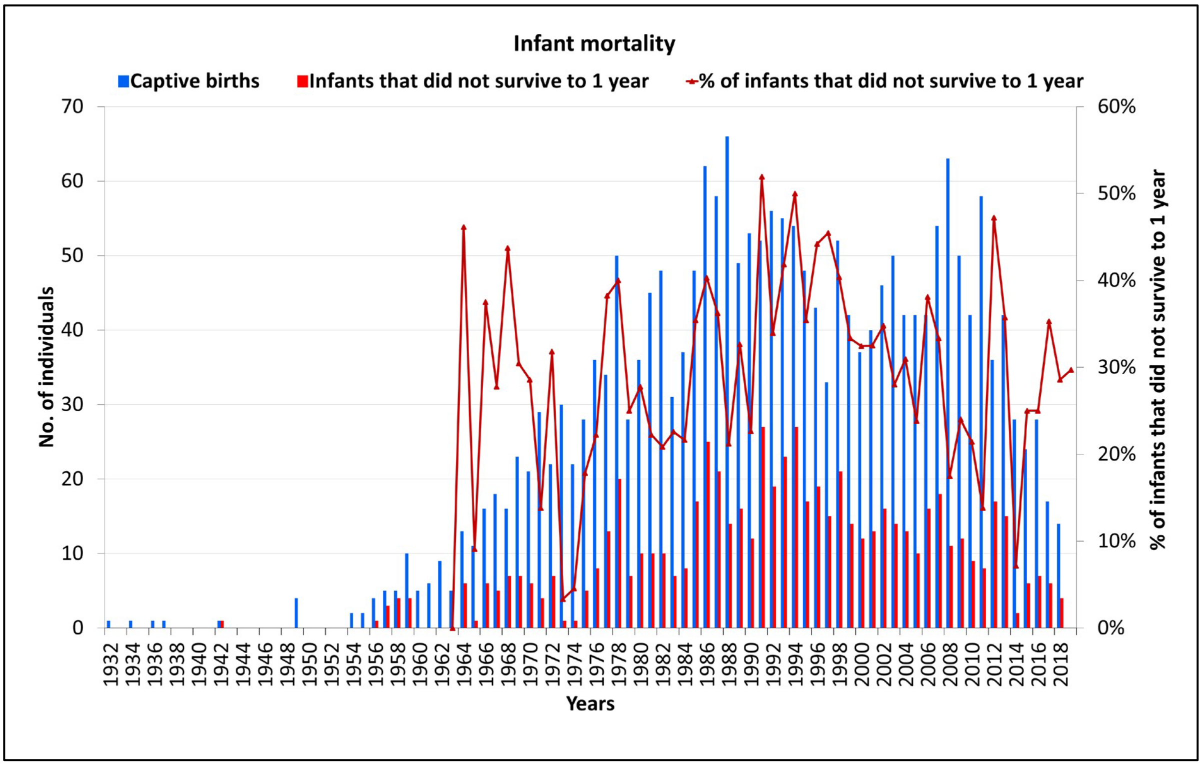


Figure 8. Annual number of births and infant deaths <1 year and % of infant deaths <1 year (sec. axis). Infant mortality is shown from 1964 onward. The number of births prior to this year was too low (<10). The data comprised a total of 2182 births with known birth dates and 658 infants that did not survive until 1 year.

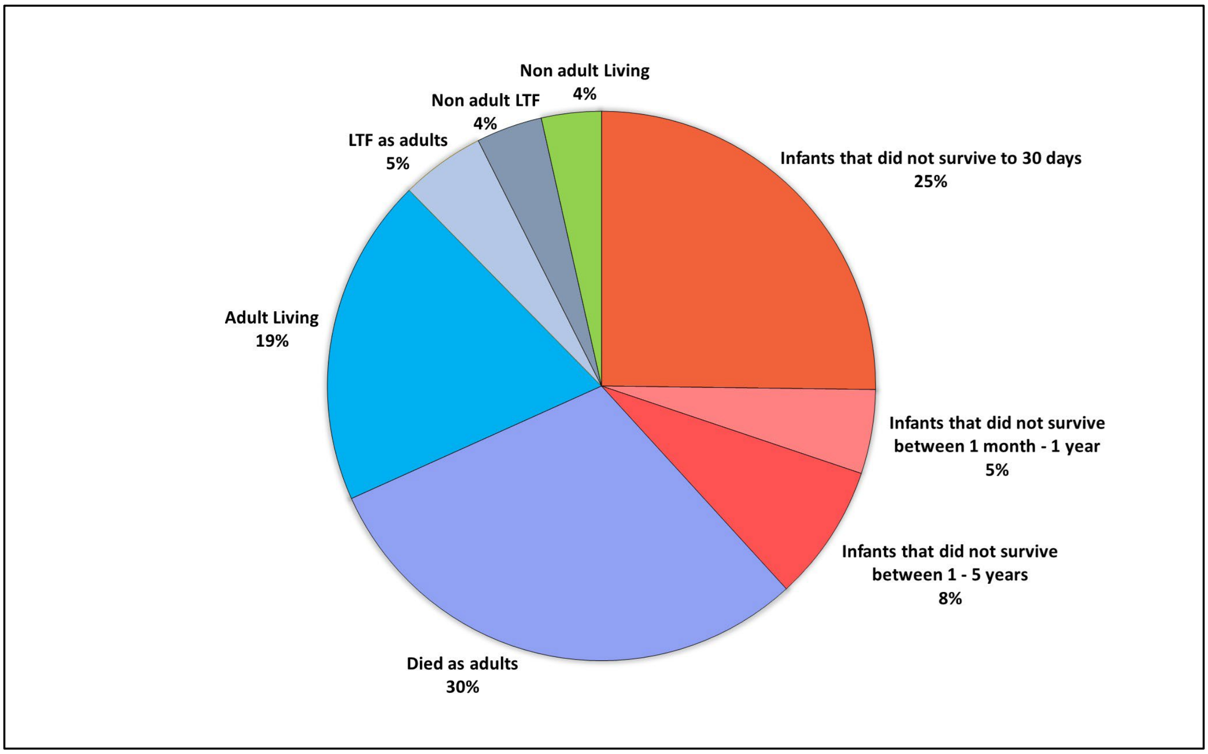


Figure 9. Pie chart showing the proportion of infants that died within - one month, one year, and five years; the proportion of adult captive-born individuals (living, dead, LTF), and the proportion of non-adult living and LTF individuals. LTF denotes ‘lost-to-follow-up’.

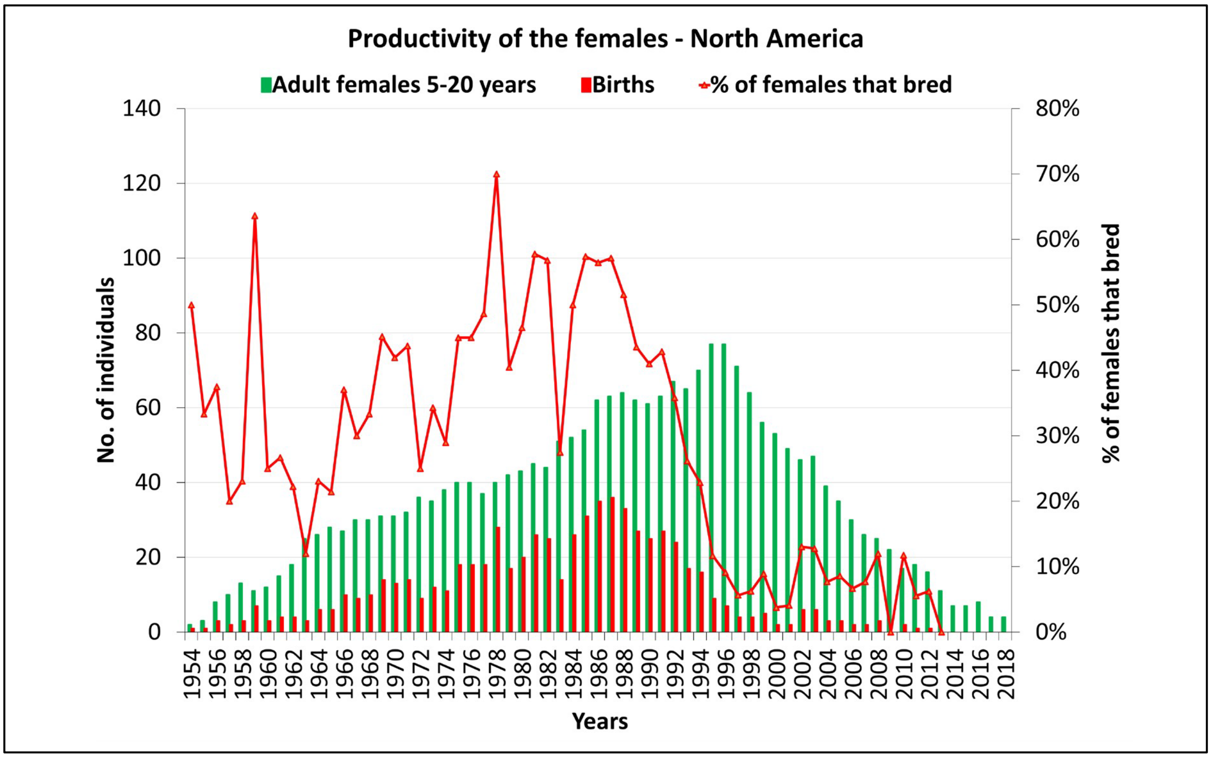


Figure 10. Annual number of adult females 5–20 years, births and percentage of females that bred – Global.

Figures 11 and 12 show that in the North American and European subpopulations, the effects of birth control are reflected in the decreasing number of females giving birth from 1989 and 2011 onward, respectively. In North America and Europe, during the most productive periods of the populations and prior to the implementation of birth control measures (1975–1988 in North America and 1986–2011 in Europe), annually a mean of 51±10% and 44±9%, respectively, of the adult females bred.

The number of institutions housing adult females globally increased overall, reaching a maximum of 82 in 1998; the numbers have been declining since then, and currently 60 institutions worldwide have females of 5–20 years of age. A mean of 34±11% (median 35%; range 13–59%) of institutions housing adult females recorded births each year from 1954 to 2018. A maximum of 36 institutions globally have recorded births in a single year (1992). A decline in interest in breeding the species is reflected in the declining trend of zoos to record breeding; in 2017 and 2018, only 18% (n = 11) of zoos housing adult females (n = 60) recorded births each year—the lowest since 1963. Similar to the global population, a mean of 31.1±22% of zoos in North America (1954–2018) and 44.1±16.8 % zoos in Europe (1956–2018) that kept adult female lion-tailed macaques bred each year.

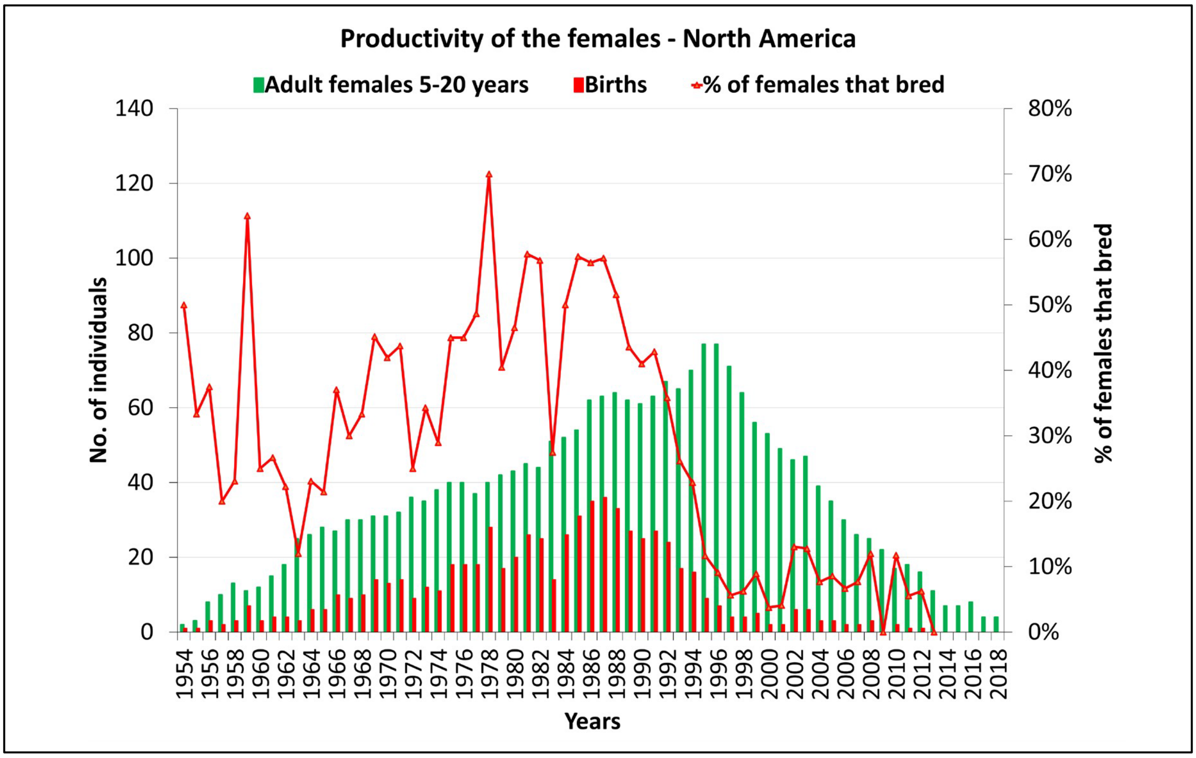


Figure 11. Annual number of adult females 5–20 years, births and percentage of females that bred – N. America.

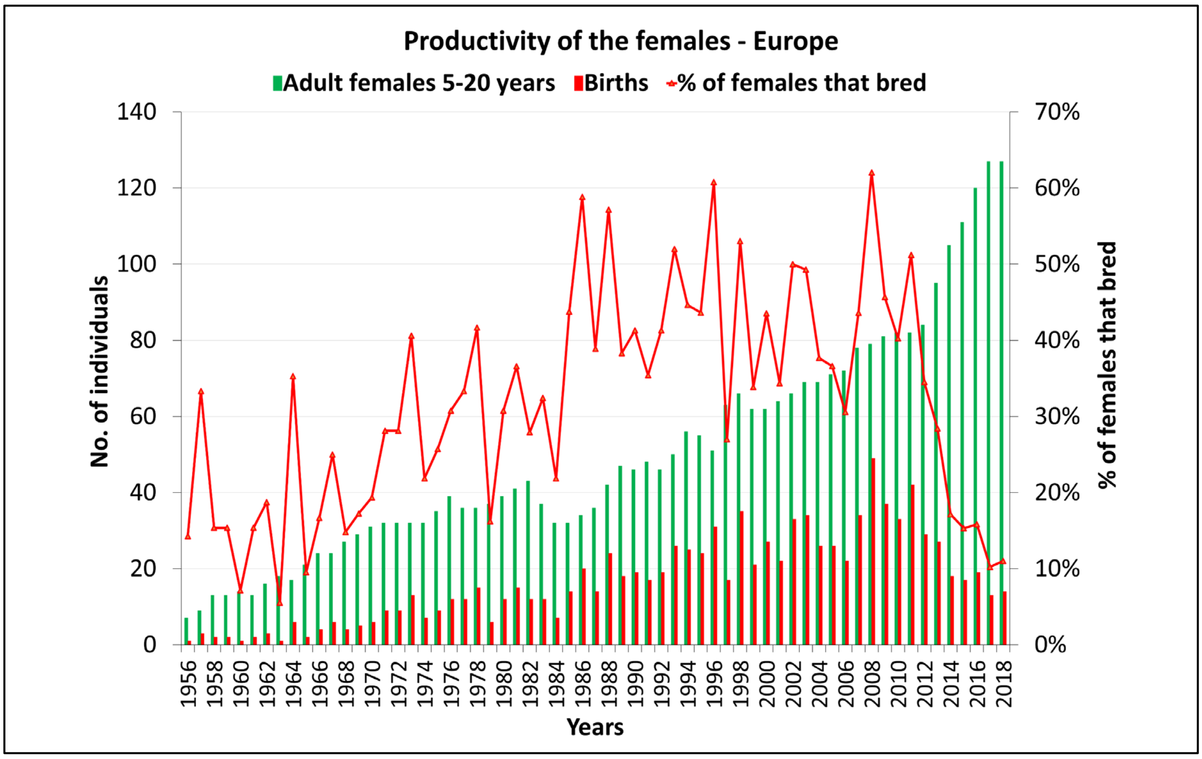


Figure 12. Annual number of adult females 5–20 years, births and percentage of females that bred – Europe.

Discussion

The individuals of the global historical captive population of the lion-tailed macaque have been recorded in zoos for more than a hundred years. Following an initial period of dependence on wild-caught individuals, the population has persisted without input from the wild till today, over about 60 years. Descendants of the wild-born individuals constituted a small, widely dispersed population via breeding that from about the 1960s onward grew slowly but steadily, largely organized in two main subpopulations. This productive period with a steady but oscillating increase in the number of births recorded worldwide a number of individuals per year larger than 200, finally increasing to more than 600 in 2011. It is likely that in this period the global population included several groups with rich demographic and social structures. The number of births and group sizes increased, providing appropriate socialization conditions (see Kaumanns *et al.* 2013; Lindburg and Gledhill 1992). Overall living conditions improved (enclosures, food, veterinary care) as is reflected in EEP and SSP reports and mortality records. Population growth and a strong increase in the number of births till about the early 1980s occurred prior to the establishment of breeding programs. Efforts to improve the captive status of the species evidently emerged from a motivation to contribute to its conservation (Hill 1971; Lindburg 2001; Singh *et al.* 2009).

In the past (in periods without population control), the global population and the individual subpopulations grew, although their overall productivity was low. Over several decades, even in the productive period, the number of births was only slightly higher than the number of deaths and overall infant mortality was high. Further, the number of females that bred was low and the number of institutions where breeding occurred per year was also low. It is likely that many breeding units revealed poor demographic and social conditions. The population likely remained in a critical status.

Systematic management in two breeding programs was carried out based on different management paradigms only during the last four decades. In both programs, there was a shortage of holding spaces for lion-tailed macaques, and birth control and other measures to reduce population size were implemented. In North America, it started a few years after the establishment of the American breeding program (Lindburg and Gledhill 1992); in Europe more than 20 years after the establishment of the European breeding program (see Sliwa *et al.* 2016).

The North American subpopulation, consequently, shrunk to a small, non-breeding stock, and the European subpopulation currently reveals a strong decrease in the number of births, and stagnates in size. Evidently with the loss of many individuals with breeding potential and further birth control measures in the remaining population, the potential for persistence of the global population decreased. A decrease in phenotypic and genetic diversity is likely although some of the individuals removed from the North American population bred at other places, for example, in Japan and Europe. A potential for "recovery" toward a larger and more diversified global population, however, may have remained. The European breeding program still manages a population of lion-tailed macaques, which forms 60% of the global population. The species is still considered of conservation concern and is expected to have breeding potential (see Sliwa *et al.* 2016).

The overall and continuing low productivity in the global population demonstrates that breeding problems that were regarded as a key problem in the captive propagation of the lion-tailed macaques for decades (Lindburg *et al.* 1989) are still virulent. They might have been temporarily, and possibly still are, "hidden" behind birth control measures. From about 1990 onward, the management of space problems overruled the discussion of breeding problems.

The development of the North American subpopulation with a background of strict genetic management (Foose and Conway 1985; Lindburg 2001) based on the "small population paradigm" (see Caughley 1994) demonstrates the risks of population management that does not intend to investigate the reasons for the decline of, and the problems in, a small population as suggested by the "declining population paradigm" (Caughley 1994). According to Flather *et al.* (2011), declining populations of animals can probably decline further due to a failure to identify and treat the causes of decline, and this failure is often related to political issues. The North American population was rapidly reduced via birth control, exports to other regions, and increasing generation time in the remaining individuals (Gledhill 1989; Fitch-Snyder 1990; Gledhill 1992; Lindburg and Gledhill 1992; Lindburg *et al.* 1997). It was believed that the wild population was less threatened than was thought earlier and that the North American captive population was secure, and a much smaller population managed toward appropriate genetic diversity would, therefore, be enough to provide a hedge against the disappearance of the species in the wild ("Hedge-breeding", see Lindburg 2001). Little consideration was given to the consequences for the behavioral components of the reproductive system of the species and the reproductive potential of the population overall (see Lindburg and Gledhill 1992; Lindburg 2001). Subsequent efforts to induce breeding in selected groups and females, respectively, remained unsuccessful (Gledhill 1990; Carter and Ness 2012). The drastic manipulations of the reproductive system as required by the hedge-breeding concept might have directly or indirectly, willingly, or unwillingly, reduced the breeding potential of the individuals (see Penfold *et al.* 2014) and the motivation of the holders to keep the species (see Lindburg 2001). Referring to this, we support Traill *et al.* (2010, p.32) who, in discussing minimum viable population sizes, noted that "many existing conservation programs might therefore be managing inadvertently or implicitly for extinction."

The steady-state/hedge-breeding management plan did not work out successfully and resulted in unexpected new logistical and practical problems (for details see Lindburg and Gledhill 1992). According to Lindburg (1993) the work with lion-tailed macaques at that time seemed to be influenced by a loss of interest in the captive propagation of macaques in North America. Attitudes toward keeping macaques were negatively influenced by space problems and incidences of Herpes B virus in some research facilities, although with no human fatalities documented in the zoos (Ness 2013). The North American breeding program for the lion-tailed macaque has been downgraded (see Lindburg 2001; Carter and Ness 2012) and is evidently not likely to achieve its original goal to have a viable captive population in American zoos (see Foose and Conway 1985).

Field studies have shown that lion-tailed macaques have a slow turnover between generations, with a late onset of breeding, few infants per female lifetime but low infant mortality (Kumar 1987; Singh *et al.* 2001; Sharma 2002; Krishna *et al.* 2006). These traits may impede the recovery of a (local) population after severe and rapid losses in terms of offspring or adults due to, for example, catastrophic events such as extreme food shortage in dry periods in the wild. Local populations may rapidly decline as a consequence. Umapathy and Kumar (2000, 2003) found that reproductive output in lion-tailed macaque groups in small fragments is lower than those in large fragments. Further risks for the survival of the species emerge from its small range of occupancy and habitat specialization.

Large scale and long-term birth control or periods of non-breeding in captivity evidently led to similar effects, thus rendering the captive population as a model for the study of coping problems related to the reproductive system of the species. For possible negative physiological consequences for the breeding potential of females, see Penfold *et al.* (2014).

The current global captive population of the lion-tailed macaque is probably more vulnerable than it might have been when the two large subpopulations were both functional. Possible negative effects of the extended birth control program in the European population cannot be excluded and may lead to a loss of breeding potential in the aging females, and in females that were not allowed to breed for a long time (see Brown *et al.* 2004; Hermes *et al.*

2004; Wachter *et al.* 2011; Penfold *et al.* 2014; Ludwig *et al.* 2019). Future management toward the persistence of the population, especially for the maintenance of a reserve, should consider this and put more emphasis on the reproductive system of the species. It should emphasize the function of the captive population as a "breeding device" (Kaumanns *et al.* 2020). The permanently low proportion of the number of females to breed and low infant survival point to mismatches between living conditions (social and non-social environment) in zoos and species-typical adaptations (see Schulte-Hostedde and Mastromonaco 2015). To achieve long-term persistence, the breeding conditions specifically need to be improved. Besides integrated genetic management (Kaumanns *et al.* 2020) this would require better behavioral and social management, in particular with reference to the strong, permanent bonds between the females and the resulting life history patterns (see Wrangham 1980; Lindburg 1991; Singh and Sinha 2004; Thierry et al. 2004). Ongoing analyses reveal that demographic structures in the historical global population failed to provide for fully appropriate conditions for the development of these adaptive patterns. For instance, group size and composition often did not allow the development of female-bonded structures. In the European population, breeding success increased with the number of large, and socially more differentiated groups (Kaumanns *et al.* 2013). In the North American population, just a few large groups contributed disproportionately to breeding and population growth (Lindburg 1992; Lindburg and Gledhill 1992), also indicating the importance of group size and demographic structures. A detailed analysis of the patterns of reproduction and their determinants, is currently ongoing.

Conclusions

The analysis of the history of the global captive population of the lion-tailed macaque revealed a potential toward population growth and persistence. The population, however, remained vulnerable; possibly related to its management. Its status from the establishment of the breeding programs onward, would have profited from global meta-population management covering at least the two large subpopulations. The management should have considered the reproductive biology of the species more strongly, including traits that evolved in its evolutionary history (see Hendry *et al.* 2011; Lankau *et al.* 2011). To improve management, the principles of an "adaptive management" *sensu* Walters and Hilborn (1978) and Walters (1997) should be considered. The effects of management measures should be monitored regularly (see Moreno Rivas *et al.* 2018 for the management of captive gorilla populations). In the lion-tailed macaque population, a coordinated international approach following the principles of the "declining population" paradigm (see Caughley 1994; Kaumanns *et al.* 2020) with the intention of improving breeding conditions before birth control and other invasive measures to control population size were carried out might have prevented the loss of precious breeding and conservation potential. It is evident that relevant management decisions depend on the "human factor", and the latter is more and more "pressured" by a lack of holding spaces. The lion-tailed macaque can serve as a model for dealing with the resulting dilemma that hinders the establishment and the use of captive populations as a reserve: sustainable populations depend on breeding and have to be large and therefore require space. Insufficient consideration of these aspects can lead to conditions that do not match with the adaptive potential of the species. A perspective for the future of a global captive population of the lion-tailed macaque that directly contributes to the conservation of the species needs to be developed. In addition to the existing cooperation with the Indian conservation science community, strengthening the cooperation between Indian and European zoos also following the one-plan approach (CBSG 2011; Byers *et al.* 2013; Fritz *et al.* 2017; Hogg *et al.* 2017) is necessary. Indian zoos can play an important role as an interface for reintroductions (Begum *et al.* 2021). The wild population of lion-tailed macaques is still and increasingly Endangered (Singh *et al.* 2020). Since the analysis of the global historical captive population as well as findings from the fragmented wild population (see above) point to the critical role of traits of the social and reproductive system for coping with human-induced altered living conditions, corresponding cooperative *in situ/ex situ* research and management projects should be developed further. Investigation of the determinants of individual reproductive success would seem to be of particular importance.

The current status of the captive population is characterized by a management-induced low number of births and the risk of a decrease in breeding potential, such as occurred in the North American population. The steps to prevent a further decline and to improve the status of the captive population need to be taken soon. Since the main part of the captive population is currently managed in the European breeding program, the latter must play a leading role toward reestablishing a global approach. The EEP itself must reconsider its management approach and especially reduce birth control and propagate more breeding (see Begum *et al.* 2021). The possible space problems require more emphasis on the establishment of further international cooperation with a chance to organize more spaces and reintroductions (see Begum *et al.* 2021). The analysis of the long-term history of the global captive population reveals shortcomings concerning the validity of the currently used management concepts. The preservation of phenotypic diversity and the long-term preservation of the breeding potential of a population demands much more attention (see Kaumanns *et al.* 2013, 2020; Penfold *et al.* 2014; Kaumanns and Singh 2015).

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Supplementary Material

<http://www.primate-sg.org/storage/pdf/PC36_Suppl_material_Begum_et_al_Lion-tail_macaque.pdf>

The following tables are available:

Table S1. Origin and sex composition of the global historical captive population of the lion-tailed macaque.

Table S2. Status – sex wise.

Table S3. Status – origin wise.

Table S4. Information on birth and death dates, birth locations, and parentage information of captive-born individuals. Table S5. Information on birth and capture date estimates, dates of entry in zoos and death dates of wild-born individuals.

Table S6. Information on birth date estimates, dates of entry in zoos and death dates of unknown origin animals.

Table S7. Abbreviations of regions.

Table S8. Transfer of captive lion-tailed macaques between regions (refer to Flowchart 1 in the article).

<http://www.primate-sg.org/storage/pdf/PC36_Suppl_material_Begum_et_al_Lion-tail_macaque.pdf>

Literature Cited

Ballou, J. D., R. C. Lacy and J. P. Pollak. 2020. PMx: Software for Demographic and Genetic Analysis and Management of Pedigreed Populations (Version 1.6.2.20200110). Chicago Zoological Society, Brookfield, Illinois, USA. Website: <http://www.scti.tools>. Accessed 30 August 2020.

Begum, N., W. Kaumanns, A. Sliwa and M. Singh. 2021. The captive population of the lion-tailed macaque *Macaca silenus*. The future of an endangered primate under human care. J. Threat. Taxa 13(9): 19352–19357. Brown, J. L., D. Olson, M. Keele and E. W. Freeman. 2004. Survey of the reproductive cyclicity status of Asian and African elephants in North America. *Zoo Biol.* 23(4): 309–321.

Byers, O., C. Lees, J. Wilcken and C. Schwitzer. 2013. The one plan approach: the philosophy and implementation of CBSG's approach to integrated species conservation planning. *WAZA Mag.* 14: 2–5.

Candolin, U. and B. B. M. Wong. (eds). 2012. *Behavioural Responses to a Changing World. Mechanisms and Consequences.* Oxford University Press, Oxford, UK.

Carter, S. and T. Ness. 2012. Population Analysis & Breeding and Transfer Plan Lion-tailed Macaque (*Macaca silenus*) AZA Species Survival Plan Yellow Program. Minnesota Zoo, MN, USA and Association of Zoos and Aquariums (AZA), Silver Spring, MD, USA. 28pp.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* 63(2): 215–244. CBSG.

(ed.). 2011. Intensively Managed Populations for Conservation Workshop Report. IUCN SSC Conservation Breeding Specialist Group, Apple Valley, MN, USA. 132pp.

Dhawale, A. K., M. A. Kumar and A. Sinha. 2020. Changing ecologies, shifting behaviours: behavioural responses of a rainforest primate, the lion-tailed macaque *Macaca silenus*, to a matrix of anthropogenic habitats in southern India. *PLoS One* 15(9): 1–19.

Fitch-Snyder, H. 1990. 1990 midyear lion-tailed macaque SSP propagation group meeting. *Lion-Tales* 7: 8–9.

Fitch-Snyder, H. 2006. *International Lion-tailed Macaque Archive Studbook Macaca silenus*. San Diego Zoo, California, USA.

Flather, C. H., G. D. Hayward, S. R. Beissinger and P. A. Stephens. 2011. Minimum viable populations: is there a "magic number" for conservation practitioners? T*rends Ecol. Evol.* 26(6): 307–316.

Foose, T. J. and W. G. Conway. 1985. Models for population management of lion-tailed macaque resources in captivity (a working paper). In: *The Lion-tailed Macaque: Status and Conservation,* P. G. Heltne (ed.), pp.329–341. Alan R Liss, New York.

Fritz, J., R. Kramer, W. Hoffmann, D. Trobe and M. Unsöld. 2017. Back into the wild: establishing a migratory Northern Bald Ibis *Geronticus eremita* population in Europe. *Int.*

Zoo Yearb. 51(1): 107–123.

Gledhill, L. G. 1987. *Lion-tailed Macaque International Studbook.* Woodland Park Zoological Gardens, Seattle, WA.

Gledhill, L. G. 1989. *Lion-tailed Macaque International Studbook.* Woodland Park Zoological Gardens, Seattle, WA.

Gledhill, L. G. 1990. Species coordinator's report. *Lion-Tales* 7(1): 1.

Gledhill, L. G. 1991. *Lion-tailed Macaque International Studbook (Revised Edition).* Woodland Park Zoological Gardens, Seattle, WA.

Gledhill, L. G. 1992. Species coordinator's report. *Lion-Tales* 8(1–2): 1–2.

Heltne, P. G. (ed.). 1985. *The Lion-tailed Macaque: Status and Conservation.* Alan R. Liss, New York, USA.

Hendry, A. P. et al. 2011. Evolutionary principles and their practical application. *Evol. Appl.* 4(2): 159–183.

Hendry, A. P., K. M. Gotanda and E. I. Svensson. 2017. Human influences on evolution, and the ecological and societal consequences. *Phil. Trans. Roy. Soc. Lond. B Biol. Sci.* 372: 20160028.

Hermes, R., T. B. Hildebrandt and F. Göritz. 2004. Reproductive problems directly attributable to long-term captivity–asymmetric reproductive aging. *Anim. Reprod. Sci.* 82–83: 49–60.

Hill, C. A. 1971. Zoo's help for a rare monkey. *Oryx* 11(1): 35–38.

Hockings, K. J. et al. 2015. Apes in the anthropocene: flexibility and survival. *Trends Ecol. Evol.* 30(4): 215–222.

Hogg, C. J., A. V. Lee, C. Srb and C. Hibbard. 2017. Metapopulation management of an endangered species with limited genetic diversity in the presence of disease: the Tasmanian devil *Sarcophilus harrisii*. *Int. Zoo Yearb.* 51(1): 137–153.

Jeschke, J. M. and D. L. Strayer. 2006. Determinants of vertebrate invasion success in Europe and North America. *Glob. Chang. Biol.* 12(9): 1608–1619.

Kappelhof, J. and J. Weerman. 2020. The development of the red panda *Ailurus fulgens* EEP: from a failing captive population to a stable population that provides effective support to *in situ* conservation. *Int. Zoo Yearb.* 54(1): 102–112.

Kaumanns, W. and B. Rohrhuber. 1995. Captive propagation in lion-tailed macaques: the status of the European population and research implications. In: *Research and Captive Propagation,* U. Gansloßer, J. K. Hodges and W. Kaumanns (eds.), pp.296–309. Filander Verlag, Fürth.

Kaumanns, W. and M. Singh. 2015. Towards more individual-based and fitness-oriented captive mammal population management. *Curr. Sci.* 109(6): 1121–1129.

Kaumanns, W., M. Singh and C. Schwitzer. 2008. Primate populations in zoos: a case of fragmentation. *Primate Rep.* 76: 41–54.

Kaumanns, W., M. Singh and A. Sliwa. 2013. Captive propagation of threatened primates – the example of the lion-tailed macaque *Macaca silenus*. *J. Threat. Taxa* 5(14): 4825–4839.

Kaumanns, W., N. Begum and H. Hofer. 2020. "Animals are designed for breeding": captive population management needs a new perspective. *J. Zoo Aquar. Res.* 8(2): 76–85.

Kinnison, M. T. and N. G. Hairston. 2007. Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Funct. Ecol.* 21(3): 444–454.

Krishna, B. A., M. Singh and M. Singh. 2006. Population dynamics of a group of lion-tailed macaques (*Macaca silenus*) inhabiting a rainforest fragment in the Western Ghats, India. *Folia Primatol.* 77(5): 377–386.

Krishnadas, M., K. Chandrasekhara and A. Kumar. 2011. The response of the frugivorous lion-tailed macaque (*Macaca silenus*) to a period of fruit scarcity. *Am. J. Primatol.* 73(12): 1250–1260.

Kumar, A. 1987. The Ecology and Population Dynamics of Lion-tailed Monkeys (*Macaca silenus*) in South India. PhD thesis, Cambridge University, Cambridge, UK.

Kumar, A., G. Umapathy and A. Prabhakar. 1995. A study on the management and conservation of the small mammals in fragmented rainforests of Western Ghats, south India: a preliminary report. *Primate Conserv.* (16): 53–58.

Kumar, M. A., S. Vijayakrishnan and M. Singh. 2018. Whose habitat is it anyway? Role of natural and anthropogenic habitats in conservation of charismatic species. *Trop. Conserv. Sci.* 11: 1–5.

Kumara, H. N. and A. Sinha. 2009. Decline of the endangered lion-tailed macaque in the Western Ghats, India. *Oryx* 43(2): 292–298.

Kumara, H. N., R. Sasi, R. Suganthasakthivel, M. Singh, H. S. Sushma, K. K. Ramachandran and W. Kaumanns. 2014. Distribution, demography, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anamalai Hills landscape, Western Ghats, India. *Int. J. Primatol.* 35(5): 976–989.

Lankau, R., P. S. Jørgensen, D. J. Harris and A. Sih. 2011. Incorporating evolutionary principles into environmental management and policy. *Evol. Appl.* 4(2): 315–325.

Lees, C. M. and J. Wilcken. 2009. Sustaining the ark: the challenges faced by zoos in maintaining viable populations. *Int. Zoo Yearb.* 43(1): 6–18.

Leus, K., L. B. Lackey, W. van Lint, D. De Man, S. Riewalt, A. Veltkam and J. Wijmans. 2011. Sustainability of European Association of Zoos and Aquaria bird and mammal populations. *WAZA Mag.* 12: 11–14.

Lindburg, D. G. 1980. Status and captive reproduction of the lion-tailed macaque *Macaca silenus*. *Int. Zoo Yearb.* 20(1): 60–64.

Lindburg, D. G. 1991. Ecological requirements of macaques. *Lab. Anim. Sci.* 41(4): 315–322.

Lindburg, D. G. 1992. Group size for captive lion-tailed macaques. *Lion-Tales* 8(1–2): 4–5.

Lindburg, D. G. 1993. Macaques may have a bleak future in North American zoos. *Zoo Biol.* 12(5): 407–409.

Lindburg, D. G. 2001. A century of involvement with lion-tailed macaques in North America. *Primate Rep.* 58: 51–64.

Lindburg, D. G. and K. A. Forney. 1992. Long-term studies of captive lion-tailed macaques. *Primate Rep.* 32: 133–142.

Lindburg, D. G. and L. Gledhill. 1992. Captive breeding and conservation of lion-tailed macaques. *Endang. Species Update* 10(1): 1–4.

Lindburg, D. G. and N. C. Harvey. 1996. Reproductive biology of captive lion-tailed macaques. In: *Evolution and Ecology of Macaque Societies,* J. E. Fa and D. G. Lindburg (eds.), pp.318–341. Cambridge University Press, Cambridge.

Lindburg, D. G., A. M. Lyles and N. M. Czekala. 1989. Status and reproductive potential of lion-tailed macaques in captivity. *Zoo Biol. Suppl.* 1: 5–16.

Lindburg, D. G., J. Iaderosa and L. Gledhill. 1997. Steady-state propagation of captive lion-tailed macaques in North American zoos: a conservation strategy. In: *Primate Conservation: The Role of Zoological Parks,* J. Wallis (ed.), pp.131–149. Special Topics in Primatology, Volume 1. American Society of Primatologists, Chicago, IL.

Lindenmayer, D. B. et al. 2012. Value of long-term ecological studies. *Austral. Ecol.* 37(7): 745–757.

Ludwig, C., M. Dehnhard, S. Pribbenow, S. Silinski-Mehr, H. Hofer and B. Wachter. 2019. Asymmetric reproductive aging in cheetah (*Acinonyx jubatus*) females in European zoos. *J. Zoo Aquar. Res.* 7(2): 87–93.

Mason, G., C. C. Burn, J. A. Dallaire, J. Kroshko, H. McDonald Kinkaid and J. M. Jeschke. 2013. Plastic animals in cages: behavioural flexibility and responses to captivity. *Anim. Behav.* 85(5): 1113–1126.

Molur, S., D. Brandon-Jones, W. Dittus, A. Eudey, A. Kumar, M. Singh, M. M. Feeroz, M. Chalise, P. Priya and S. Walker. 2003. *Status of South Asian Primates: Conservation Assessment and Management Plan (C.A.M.P.) Workshop Report.* Zoo Outreach Organisation, CBSG-South Asia, Coimbatore. 432pp.

Moreno Rivas, M., J. D. Rodríguez Teijeiro, and M. T. Abelló. 2018. Genetic and demographic analysis of European Endangered Species Programme (EEP) and Species Survival Plan (SSP) Western lowland gorilla *Gorilla gorilla gorilla* populations. *Int. Zoo Yearb.* 52(1): 194–211.

Ness, T. 2013. *North American Studbook for Lion-tailed Macaques* (*Macaca silenus*). Minnesota Zoological Gardens, Apple Valley, MN, USA.

Nowak, K. and P. C. Lee. 2013. "Specialist" primates can be flexible in response to habitat alteration. In: *Primates in Fragments II: Complexity and Resilience,* L. K. Marsh and C. A. Chapman (eds.), pp.199–211. Springer, New York.

Penfold, L. M., D. M. Powell, K. Traylor-Holzer and C. S. Asa. 2014. "Use it or lose it": characterization, implications, and mitigation of female infertility in captive wildlife. *Zoo Biol.* 33(1): 20–28.

Powell, D. M., C. L. Dorsey and L. J. Faust. 2019. Advancing the science behind animal program sustainability: an overview of the special issue. *Zoo Biol.* 38(1): 5–11.

Princée, F. P. G. 2016. *Exploring Studbooks for Wildlife Management and Conservation. Topics in Biodiversity and Conservation.* Springer Nature, Cham, Switzerland.

Reinke, B. A., D. A. W. Miller and F. J. Janzen. 2019. What have long-term field studies taught us about population dynamics? *Ann. Rev. Ecol. Evol. Syst.* 50: 261–278.

Sarno, A. 2018. *North American Studbook for Lion-tailed Macaques* (*Macaca silenus*). Kansas City Zoo, Kansas City, MO.

Schulte-Hostedde, A. I. and G. F. Mastromonaco. 2015. Integrating evolution in the management of captive zoo populations. *Evol. Appl.* 8(5): 413–422.

Scobie, P and L. Bingaman Lackey. 2012. Single Population Analysis and Records Keeping System (SPARKS) (Version 1.66). International Species Information System (ISIS, renamed to Species360). Eagan, MN, USA.

Sharma, A. K. 2002. A Study of Reproductive Behaviour of Lion-tailed Macaque (*Macaca* *silenus*) in the Rainforests of Western Ghats. PhD thesis, University of Mysore, Mysore, India.

Sih, A., M. C. O. Ferrari and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* 4(2): 367–387.

Singh, M. and W. Kaumanns. 2005. Behavioural studies: a necessity for wildlife management. *Curr. Sci.* 89(7): 1230–1236.

Singh, M. and A. Sinha. 2004. Life history traits: ecological adaptations or phylogenetic relics? In: *Macaque Societies: A Model for the Study of Social Organization,* B. Thierry, M. Singh and W. Kaumanns (eds.), pp.80–83. Cambridge University Press, Cambridge, UK.

Singh, M., M. Singh, H. N. Kumara, M. A. Kumar and L. D'Souza. 1997. Inter and intra-specific association of non-human primates in Anaimalai Hills, south India. *Mammalia* 61: 17–28.

Singh, M., M. Singh, M. A. Kumar, H. N. Kumara, L. D'Souza and B. A. A. K. Sharma. 1998. Behaviour of lion-tailed macaque (*Macaca silenus*) in vulnerable and relatively secure habitats in the rainforests of Western Ghats, India. *Tigerpaper* 25(4): 19–25.

Singh, M., H. N. Kumara, M. A. Kumar and A. K. Sharma. 2001. Behavioural responses of lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rain forest fragment in the Western Ghats, India. *Folia Primatol.* 72(5): 278–291.

Singh, M., M. Singh, M. A. Kumar, H. N. Kumara, A. K. Sharma and W. Kaumanns. 2002. Distribution, population structure, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anaimalai Hills, Western Ghats, India. *Am. J. Primatol.* 57(2): 91–102.

Singh, M., A. K. Sharma, E. Krebs and W. Kaumanns. 2006. Reproductive biology of lion-tailed macaque (*Macaca silenus*): an important key to the conservation of an endangered species. *Curr. Sci.* 90(6): 804–811.

Singh, M., W. Kaumanns, M. Singh, H. S. Sushma and S. Molur. 2009. The lion-tailed macaque *Macaca silenus* (Primates: Cercopithecidae): conservation history and status of a flagship species of the tropical rainforests of the Western Ghats, India. *J. Threat. Taxa* 1(3): 151–157.

Singh, M., W. Kaumanns and G. Umapathy. 2012. Conservation-oriented captive breeding of primates in India: is there a perspective? *Curr. Sci.* 103(12): 1399–1400.

Singh, M., A. Kumar and H. N. Kumar. 2020. *Macaca silenus*. The IUCN Red List of Threatened Species 2020: e.T12559A17951402. <http://www.iucnredlist.org>. Accessed 16 July 2021.

Sliwa, A. and N. Begum. 2019. *International Studbook 2018 for the Lion-tailed Macaque Macaca silenus Linnaeus, 1758, Edition 2018 – Volume 9.* Zoologischer Garten Köln, Köln, Germany.

Sliwa, A., K. Schad and E. Fienig. 2016. Long-term Management Plan for the Lion tailed macaque (*Macaca silenus*) European Endangered Species Programme (EEP). Zoologischer Garten Köln, Köln, Germany and European Association of Zoos and Aquaria (EAZA), Amsterdam, Netherlands. 60pp.

Soulé, M. E. 1985. What is conservation biology? *BioScience* 35(11): 727–734.

Strier, K. B. 2017. What does variation in primate behavior mean? *Am. J. Phys. Anthropol.* 162(S63): 4–14.

Sushma, H. S. and M. Singh. 2006. Resource partitioning and interspecific interactions among sympatric rain forest arboreal mammals of the Western Ghats, India. *Behav. Ecol.* 17(3): 479–490.

Sushma, H. S., R. Mann, H. N. Kumara and A. Udhayan. 2014. Population status of the endangered lion-tailed macaque *Macaca silenus* in Kalakad-Mundanthurai Tiger Reserve, Western Ghats, India. *Primate Conserv.* (28): 171–178.

Thierry, B., M. Singh and W. Kaumanns. (eds.). 2004. *Macaque Societies: A Model for the Study of Social Organization.* Cambridge University Press, Cambridge, UK.

Traill, L. W., B. W. Brook, R. R. Frankham and C. J. A. Bradshaw. 2010. Pragmatic population viability targets in a rapidly changing world. *Biol. Conserv.* 143(1): 28–34.

Tuomainen, U. and U. Candolin. 2011. Behavioural responses to human-induced environmental change. *Biol. Rev.* 86(3): 640–657.

Umapathy, G. and A. Kumar. 2000. The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Anamalai Hills, south India. *Primates* 41(2): 119–126.

Umapathy, G. and A. Kumar. 2003. Impacts of forest fragmentation on lion-tailed macaque and Nilgiri langur in Western Ghats, south India. In: *Primates in Fragments: Ecology and Conservation,* L. K. Marsh (ed.), pp.163–189. Kluwer Academic/Plenum Press, New York.

Umapathy, G., S. Hussain and S. Shivaji. 2011. Impact of habitat fragmentation on the demography of lion-tailed macaque (*Macaca silenus*) populations in the rainforests of Anamalai Hills, Western Ghats, India. *Int. J. Primatol.* 32(4): 889–900.

Wachter, B., S. Thalwitzer, H. Hofer, J. Lonzer, T. B. Hil- debrandt and R. Hermes. 2011. Reproductive history and absence of predators are important determinants of reproductive fitness: the cheetah controversy revisited. *Conserv. Lett.* 4(1): 47–54.

Walters, C. 1997. Adaptive policy design: thinking at large spatial scales. In: *Wildlife and Landscape Ecology,* J. A. Bissonette (ed.), pp.386–394. Springer, New York.

Walters, C. J. and R. Hilborn. 1978. Ecological optimization and adaptive management. *Ann. Rev. Ecol. Evol. Syst.* 9(1): 157–188.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75(3): 262–300.

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Supplementary Materials for "A Hundred Years in Zoos: History and Development of the Captive Population of the Lion-tailed Macaque *Macaca silenus*. Long term persistence for conservation?"

by Nilofer Begum, Werner Kaumanns, Mewa Singh and Heribert Hofer

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Data available from studbook

Table S1. Origin and sex composition of the global historical captive population of the lion-tailed macaque

Birth type	**Males**	**Females**	**Unknown sex**	**Total**
Wild-born	183	209	36	428
Captive-born	1037	972	186	2195
Unknown origin	42	65	4	111
Total global historical population	1262	1246	226	2734

Table S2. Status – sex wise

Fate/status of the animals	**Males**	**Females**	**Unknown sex**	**Total**
Living	220	279	17	516
Dead	867	865	191	1923
Lost-to-follow-up	175	102	18	295
Total global historical population	1262	1246	226	2734

Table S3. Status – origin wise

Fate/status of the animals	**Captive-born**	**Wild-born**	**Unknown origin**	**Total**
Living	499	16	1	516
Dead	1499	332	92	1923
Lost-to-follow-up	197	80	18	295
Total global historical population	2195	428	111	2734

Table S4. Information on birth and death dates, birth locations, and parentage information of captive-born individuals

Data for captive-born animals	**Known**	**Unknown**	**Total**
Birth dates/estimates	2182	13	2195
Birth locations	2189	6	2195
Sires	2041	154	2195
Dams	2049	146	2195
Death dates	1494	5	1499

Table S5. Information on birth and capture date estimates, dates of entry in zoos and death dates of wild-born individuals

Data for wild-born animals	**Known**	**Unknown**	**Total**
Birth date estimates	273	155	428
Capture date estimates	325	103	428
Entry dates to a zoo (for those whose capture dates were not known)	101	2	103
Death dates	329	3	332

Table S6. Information on birth date estimates, dates of entry in zoos and death dates of unknown origin animals

Data for unknown origin animals	**Known**	**Unknown**	**Total**
Birth date estimates	71	40	111
Entry dates to a zoo (for those whose birth dates were not known)	38	2	40
Death dates	92	0	92

Table S7. Abbreviations of regions

		ASIA	
EUR	Europe	IND	India
NA	North America	JAP	Japan
SA	South America	BUR	Burma
MEX	Mexico	SL	Sri Lanka
CAR	Caribbean	NEP	Nepal
AFR	Africa	MAL	Malaysia
AUS	Australia	SING	Singapore
UNK	Unknown	HK	Hong Kong
		CHI	China
		S KOR	S. Korea
		INDO	Indonesia
		PHIL	Philippines

Table S8: Transfer of captive lion-tailed macaques between regions (refer to Flowchart 1 in the article)

Transfers between regions																			
To →	EUR	NA	SA	MEX	ASIA											AFR	AUS	UNK	Total
From ↓					IND	JAP	BUR	NEP	MAL	SING	HK	CHI	SKOR	INDO	PHIL				
NA	47			4		47			1	5	4	8	8			2	7	6	139
EUR		33	1	2		4				1		2		5	6	12		1	67
India (zoos)	4	6					3	3	1	1							10		28
JAP												25						10	35
SING	3								4		1					4			12
HK	2											2							4
SL																	4		4
CAR		3																	3
SA	1																		1
UNK	31	21			16	41							1			5	1		116

Chapter 3: Publication 2

A Hundred Years in Zoos II: Patterns of Reproduction in the Global Historical Captive Population of the Lion-tailed Macaque *Macaca silenus*

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Contributions of the authors

The conceptual framework and the manuscript of the study were developed by Nilofer Begum and Werner Kaumanns. Nilofer Begum carried out the organisation, and analysis of data and the visualisation of the results. Heribert Hofer contributed to the approach of the study. He also contributed ideas and means to analyse and visualise the distribution of group sizes. Mewa Singh extensively commented on the manuscript and in particular to the discussion of *in situ* – *ex situ* comparisons and the use of statistics.

Primate Conservation 2023 (37)

A Hundred Years in Zoos II: Patterns of Reproduction in the Global Historical Captive Population of the Lion-tailed Macaque *Macaca silenus*

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Abstract: This study investigates the patterns of reproduction and the distribution of group sizes in the global historical captive population of the lion-tailed macaque. It is based on the species' international studbook. We analyzed individual reproductive output, infant mortality, group sizes and transfers of individuals as determinants of the development of the population and its productivity. Since direct information on groups and their management is not available for the majority of the zoos, we use the individuals recorded per location as a proxy for a group. We expected deviations in the parameters investigated with reference to corresponding findings from the wild. They are discussed under the perspective of mismatches between species-typical adaptations and captive conditions, which might result in low productivity and breeding problems. Results show that the overall productivity of the population was low: a large proportion of the females did not breed at all—sometimes due to birth control. Females that bred showed a large variation in reproductive output. Infant mortality was high. During all periods, most zoos kept small numbers of individuals, which allowed for the formation of only small groups—deviating demographically from the larger female-bonded groups in the wild. The (social) stability of captive groups was impeded by transfers of females between institutions. In the wild, females are philopatric, remaining in their natal groups. The possible consequences of the deviations regarding their social life are discussed. We suggest that the female-bonded social system is a key trait to be considered for the management of the captive population.

Keywords: Lion-tailed macaque, endangered species, global historical captive population, patterns of reproduction, individual reproductive output, groups

Introduction

The Endangered lion-tailed macaque (*Macaca silenus*), endemic to the Western Ghats in southern India, is threatened because of habitat destruction and fragmentation (Singh *et al.* 2020). The species has been kept in zoos for more than a hundred years—an estimated 2,734 individuals in 366 institutions (Sliwa and Begum 2019). The zoo population was, and still is, highly fragmented, and in conditions strongly disparate from its natural habitats. The resulting current captive population seems to have a low potential for sustainability (see Begum *et al.* 2022). In this study, we emphasize the endangered status of both the wild and captive populations. A conservation-oriented international breeding program for the species was established in the 1980s, with the intention of developing a captive population as a reserve (Conway 1985). By systematically managing breeding, the aim was to increase the size of the population even while taking measures to reduce populations in certain regions via birth control. Especially in the early but also in the later decades, the living and breeding conditions provided for the macaques were poor (see Lindburg 1992; Kaumanns and Rohrhuber 1995) and, it would seem, negatively influenced the productivity—the number of surviving infants per adult female—of the global historical population. Comparisons with the reproductive patterns of females in the wild, therefore, are likely to reveal the management-induced disparity. Regarding the species' conservation, it is essential to investigate the nature of potential deviations and to assess whether the patterns of reproduction in the captive population are likely to support the long-term persistence required for a reserve.

The global historical captive population comprised two main subpopulations—in North America and in Europe—and a few smaller ones, besides others, in India and Japan. Although it grew slowly over the decades, it has not to date achieved a secure status. For a recent analysis of its history, development and status see Begum *et al.* (2022). Begum *et al.* (2022) and previous studies focusing on earlier time periods point to low productivity at the population level, high infant mortality, and breeding problems (Heltne 1985; Lindburg 1980, 2001; Lindburg *et al*. 1989; Lindburg and Forney 1992; Lindburg and Gledhill 1992; Kaumanns and Rohrhuber 1995; Kaumanns *et al*. 2001, 2006, 2008, 2013). The current population may not be sufficiently productive to function as a future reserve; the potential for sustainability appears to be low.

In addition to possible special reasons for breeding problems (such as poor health of the females), we propose that large discrepancies in the living conditions in the wild and those in zoos might have contributed to the unsatisfactory development of the global historical population. According to Schulte-Hostedde and Mastromonaco (2015), altered living conditions can lead to mismatches with traits evolved in the past and can result in coping problems and maladaptive developments. The authors, for instance, point to the role of opportunities for mate choice that, if lacking, can negatively influence reproductive success. Several authors, Hendry *et al.* (2011), Candolin and Wong (2012), Mason *et al*. (2013), Sih *et al*. (2011) and Sih (2013), use the term “mismatch” in studies on the effects of altered living conditions on animals and plants. A growing field of research focuses on Human-induced Rapid Environmental Change (HIREC) (Sih *et al*. 2011). Mason *et al*. (2013) even used the term Captivity-induced Rapid Environmental Change (CIREC) to focus on the discrepancies between captive living conditions and adaptations in animal species.

For the present study, it is assumed that the identification of mismatches that lion-tailed macaques possibly experience in zoos is critical for management aiming at the persistence of the population. The identification of mismatches is unlikely to lead to a causal understanding of, for instance, breeding problems, but it would facilitate the design of more focused investigations on the latter and contribute to more appropriate global management approaches that consider the biology of the species. It might also provide hints on potential conservation issues in the fragmented wild population. Umapathy and Kumar (2000, 2003) found that fragmentation can cause a reduction in birth rate and subsequently in the proportion of juveniles. The challenge concerning the conservation of lion-tailed macaques is the management of small and isolated populations (Singh and Kaumanns 2005).

Low reproductive output in the fragmented captive population of the lion-tailed macaque is likely to be a consequence of poor breeding of the individuals, high infant mortality and—in the last decades—birth control measures on a large scale. Reproductive patterns of captive populations are evidently influenced by the management-induced ‘artificial’ living conditions, that temporarily induce lack of breeding opportunities in the absence of fertile partners (see Nuss and Warneke 2010). Previous studies on captive lion-tailed macaques point to the importance of the quality of the breeding units, including size, composition, and the resulting potential to allow for species-typical behavior concerning reproduction and successful breeding (Lindburg 1992; Singh and Kaumanns 2005; Kaumanns *et al.* 2006, 2013). The critical alterations in the living conditions of the captive lion-tailed macaques may be largely demographic (for example, group size) and social in nature. We believe that the groups in which the individuals of the global historical captive population were kept did not correspond to those in groups in the wild. Individuals in the captive groups possibly lack the demographic conditions to realize their species-typical traits, which include a female-bonded social system.

Aims

In this study we investigate the patterns of reproduction in the global historical captive population of the lion-tailed macaque, examining particularly individual reproductive output, and identifying how living conditions might establish mismatches with species-typical adaptations. The investigation considers individuals, groups, regions, time, management periods, and selected aspects of the demography of the population, including the distribution of group sizes and the management-induced population dynamics via transfer of individuals between groups.

We provide detailed descriptions of our results to provide reference data and other relevant findings for future population management, not only of lion-tailed macaques but also for other primate species, indicating the complexity of the history of a population that is designed as a reserve. We refer to Sheldon *et al.* (2022), who point to the value of individual-based, long-term studies to provide data that can be used for future studies with new research questions (see also Clutton-Brock and Sheldon 2010).

The only source of data for the global captive population of the lion-tailed macaque reaching back over the full time of its existence is its international studbook (Sliwa and Begum 2019). Studbooks are a rich source of data for population analysis (Princée 2016), even with certain limitations (see below).

Methods

We used the most recent international studbook of the lion-tailed macaque (Sliwa and Begum 2019), and the previous version of Fitch-Snyder (2006), which provide records on the 2,734 registered lion-tailed macaques kept in 366 zoos since 1899. The data is current until 2018. This sample covers the entire known captive population of the species. The zoos were distributed over 54 countries, mainly in Europe, North America, and Asia. In the early decades, the colonies were managed locally. Since 1983, the North American subpopulation was based on a regional studbook and managed in a specific breeding program (Species Survival Plan, SSP), with strict genetic management and control of population size via large-scale birth control introduced a few years after the plan was drawn up (see Lindburg *et al.* 1997). Since 1989, the European subpopulation has been managed in an equivalent European Endangered Species Program (EEP). The EEP was more behavior-based and oriented toward the establishment of large, species-typical groups (Kaumanns *et al.* 2013). Large-scale birth control measures were initiated in Europe much later, from about 2012 onward (see Kaumanns *et al.* 2013; Sliwa *et al.* 2016; Begum *et al.* 2022). Judging from the management recommendations of the two programs, it can be concluded that birth control measures were carried out in many colonies in the two regions (Lindburg 2001; Sliwa *et al.* 2016), but it is usually impossible to identify when and with which individuals they were started and ended. A similar situation was noted by Nuss and Warneke (2010) in their analysis of captive populations of Goeldi's monkeys.

Our study was based on studbook records for individual lion-tailed macaques that included birth dates, capture dates/estimates, birth type (wild-born, captive-born or of unknown origin), sex, location, the parentage, and dates of death and transfers between locations and regions. The studbook does not provide systematic information about contraception and no systematic information about hand-rearing. The studbook provides records for the individuals (see below) but no direct information on the social units in which they were kept. It only informs about where the individuals were located over time. According to zoo journals and annual reports (*Lion-Tales* in North America and EEP Yearbooks in Europe), most individuals in the zoos and collections were kept as a group, but further reliable information is generally unavailable. Kempske (1985) mentioned zoos that temporarily kept more than one group. Demographic data referring to a location, as derived from studbooks (see Princée 2016), however, can indirectly provide information about the potential to establish social relationships, partner constellations, and a number of other behavior-based aspects that are relevant for the establishment of species-typical life history patterns. The latter themselves influence productivity and the persistence of a population (Stearns 2000; Singh and Kaumanns 2005; Kaumanns *et al.* 2020). Considering this, we used the total of individuals recorded in a location as a proxy for a group and analyze the distribution of group sizes in the population. The number of individuals per location is used to discuss the potential to realize species-typical behavior and social structures and to successfully reproduce. The distribution of group sizes can provide hints on the overall reproductive potential of the population. It is evident, however, that the latter is influenced by more factors than just "group size", for instance by enclosures, food, health conditions, husbandry systems, and approaches of zoos toward conservation and welfare. An influence of these factors on the chances of a female to reproduce is likely but cannot be deduced from the studbook records. The potential of the study to go beyond a descriptive approach is therefore limited. Due to these limitations, and also due to potentially confounded variables to influence breeding, the study focuses on the identification of critical features of the population with reference to mismatches and conditions for low productivity. The number of individuals per location (used as a proxy for a group) is regarded as a critical trait of the population for the study. The following topics are considered for the identification of mismatches: 1) a description of the individual patterns of reproduction; 2) a descriptive analysis of the distribution of groups of different sizes; 3) an analysis of the transfers of individuals between zoo colonies; and 4) the fragmented nature of the population. The results are discussed with reference to key traits in the social system of the species.

The term 'colony' is used for the total historical stock of lion-tailed macaques recorded in a zoo. Colonies may exist over decades. "Groups" are the heterosexual or monosexual social units of individuals kept together over some time. Our study assumes that in most cases individuals in a location were kept together as a group and as a breeding unit. This is often confirmed by the occurrence of births or reports and publications that refer to individual groups. Focusing on the groups, we investigate the distribution of group sizes, and aspects of their "quality" including, composition, and time (in years) during which a group existed. Transfers of females and males between groups are also included.

The lion-tailed macaque international studbook is maintained as an electronic database in the software SPARKS (Single Population Analysis and Records Keeping System *v* 1.66) (Scobie and Bingaman Lackey 2012). We used the population management program PMx *v* 1.6.2 (Ballou *et al.* 2020) for the analysis of the various demographic parameters available from the Species Conservation Toolkit Initiative (<https://scti.tools>). Data was formatted using Microsoft Excel for further analyses in R *v* 4.2.0 software (R core team 2021). The Kaplan–Meier survival analysis (Kaplan and Meier 1958) was done using the 'survival' package (Therneau 2022) in R. It was carried out for captive-born individuals with known birth dates and living/lost-to-follow-up individuals were treated as right-censored. Reproductive output of the females (infants/breeding female and surviving infants/breeding female) was compared between locations and regions using Kruskal-Wallis tests. The Dunn *Post Hoc* Test was used for pairwise comparisons using Kruskal–Wallis tests when a significant difference was obtained (values of p were adjusted by Bonferroni correction). Sex difference in overall infant mortality was compared using the Chi-square Test. The Chi square Test of Multiple Proportions and Marascuilo's *Post Hoc* Test were used to compare the number of infants per adult female in the North American and European populations under different management conditions. A Wilcoxon Rank Sum Test was used to test differences between the reproductive output of captive-born adult females in natal versus non-natal groups. A p-value of ≤ 0.05 was considered significant.

Since the study covers more than 100 years, and possible developmental trends should be traced, corresponding data are analyzed and presented by decade.

Results

As a background for the analysis of the patterns of reproduction, we first summarize the demographic structure and development of the population referring to births and deaths (for a more detailed description and discussion, see Kaumanns *et al.* 2013; Begum *et al.* 2022). The reproductive output of the population is then analyzed with reference to the individuals and to the zoo colonies.

Development of the population

The historical population from 1899 to 2018, increased in size from the 1950s but decreased from 2011 onward (Fig. 1). The global population was 2,734 individuals, with 886 lion-tailed macaques in North American zoos, and 1,248 kept in European zoos, with smaller numbers in India (n = 350) and Japan (n = 303), and a few other regions (n = 222). Individuals were occasionally transferred between regions.

The global historical population was distributed over 366 institutions (mostly zoos). Their numbers grew from the 1950s to about 2004, involving 116 zoos. This growth was followed by a slight decrease, oscillating around 100 institutions. The North American subpopulation was kept in 133 and the European population in 125 institutions. Male and female lion-tailed macaques constituted the population in similar numbers. Figure 1 shows that the sex ratio remained quite constant. Overall, the number of males recorded (n = 1,262) was a little higher than the number of females (n = 1,246). The annual number of births and imports of wild-born animals and the number of adult females are shown in Figure 2. Regular breeding was recorded from 1954 onward. Overall, the number of births increased, inducing population growth together with imports of wild-caught individuals. From about 1970 onward, population growth came from captive births. From about 1990 onward, the global population size was mainly influenced by births in the European subpopulation. Till about 1995 and again during 2011–2018, there was an overall increase in the number of adult females. A corresponding increase in births occurred till 1988; and after a period of about 20 years with a fluctuating pattern in births, the numbers continuously decreased from 2011 onward. Currently, some Indian zoos keep a few rescued wild-born individuals. For more details especially annual growth rates, see Begum *et al*. (2022).

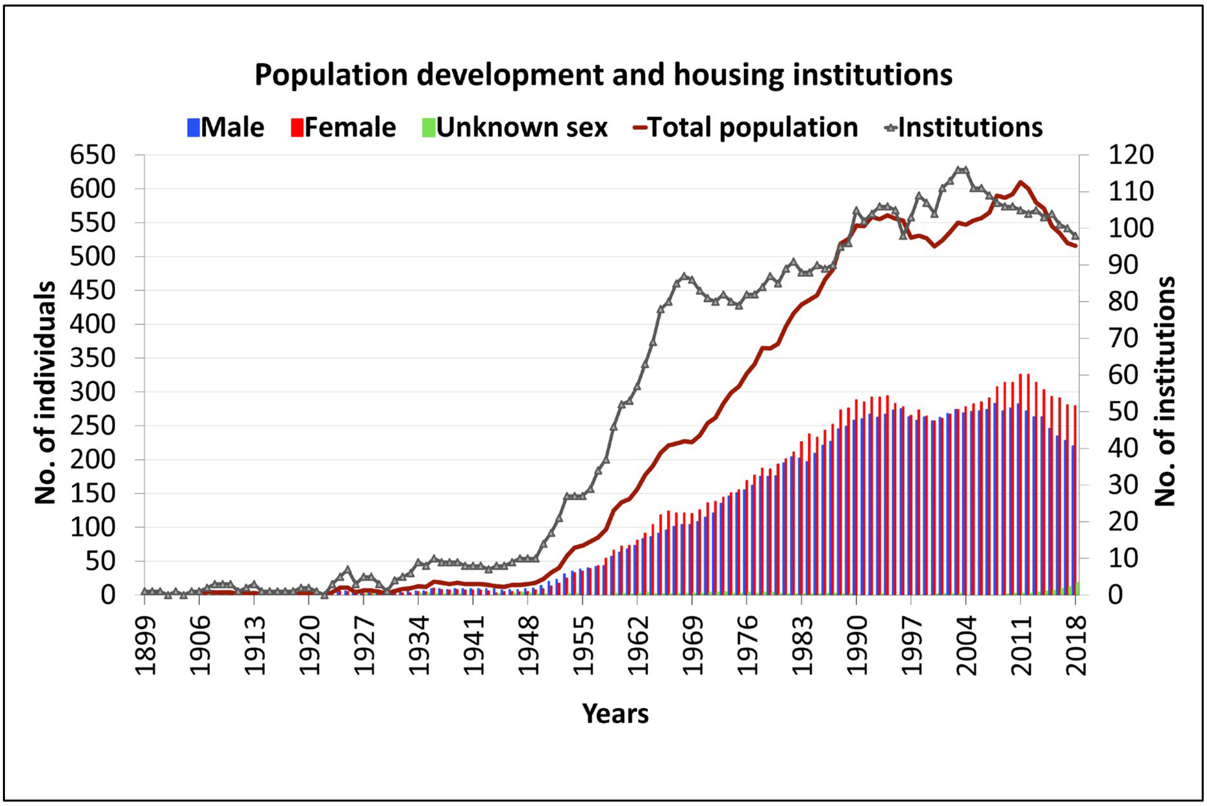


Figure 1. Population development and housing institutions

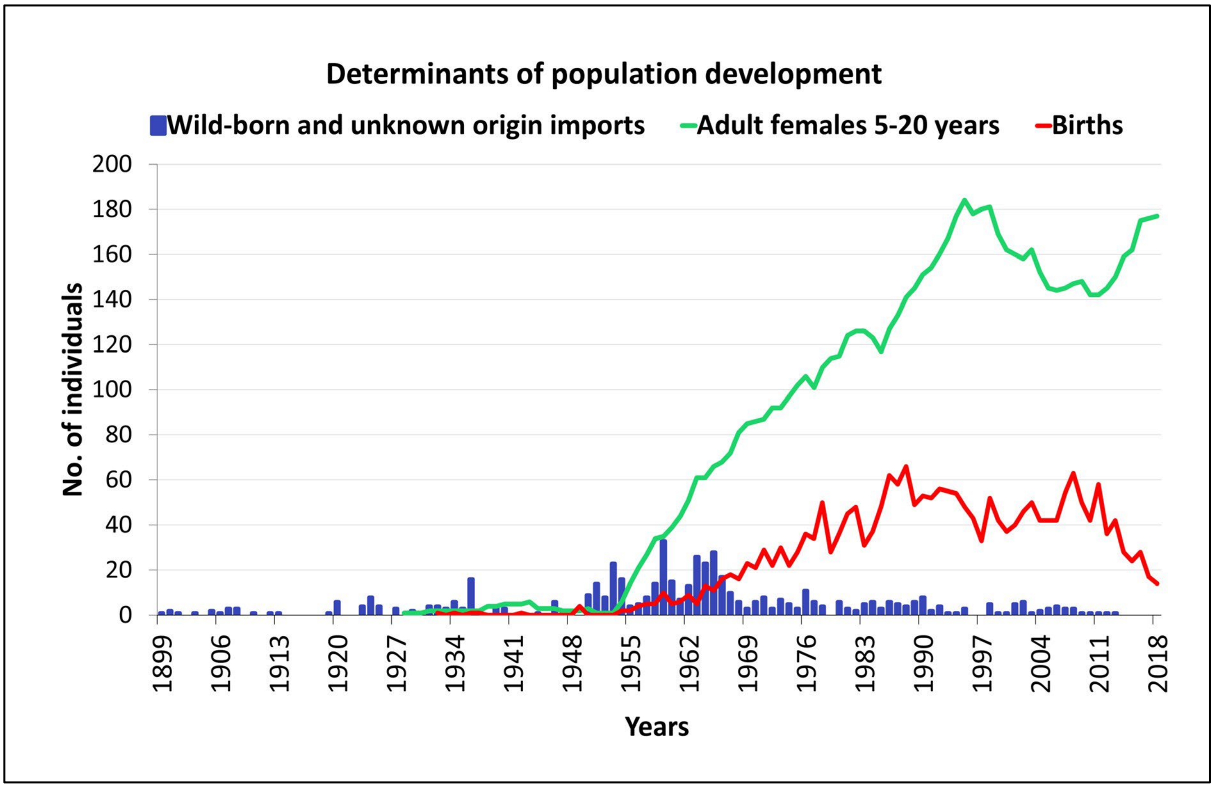


Figure 2. Annual number of births and imports of wild-born and unknown origin animals and adult females in the global population

Mortality

Figure 3 shows the Kaplan–Meier survivorship curve of captive-born lion-tailed macaques in the global historical population. It is based on 1,792 individuals with known birth dates and excludes those that did not survive the first day. The figure reveals that the survivorship of captive lion-tailed macaques was very low in the first year of life (infant mortality), before decreasing at a slower rate. The median life span was 16.2 years (95% CI 15 to 17.7; median 5897 days 95% CI 5483 to 6457). When the individuals that did not survive the first day were included in the sample (n = 2,182) the median lifespan was just over 11.5 years (95% CI 10.1 to 12.7; median 4185 days 95% CI 3702 to 4637). There was a significant difference (log-rank: $\chi^2 = 4.6$, df = 1, p = 0.03) in the life span of males (n = 872, median 16.7 years, 95% CI 15.1 to 18.5) and females (n = 838, median 17.8 years, 95% CI 15.7 to 19.1). Infant mortality was high overall, *c.*30% (n = 658), with most deaths occurring in the first month of life (n = 550) (for details see Begum *et al.* 2022). There was no significant difference ($\chi^2 = 3.30$, df = 1, p = 0.07) in infant mortality between males (*c.* 28.4%, n = 293) and females (*c.* 24.8%, n = 239).

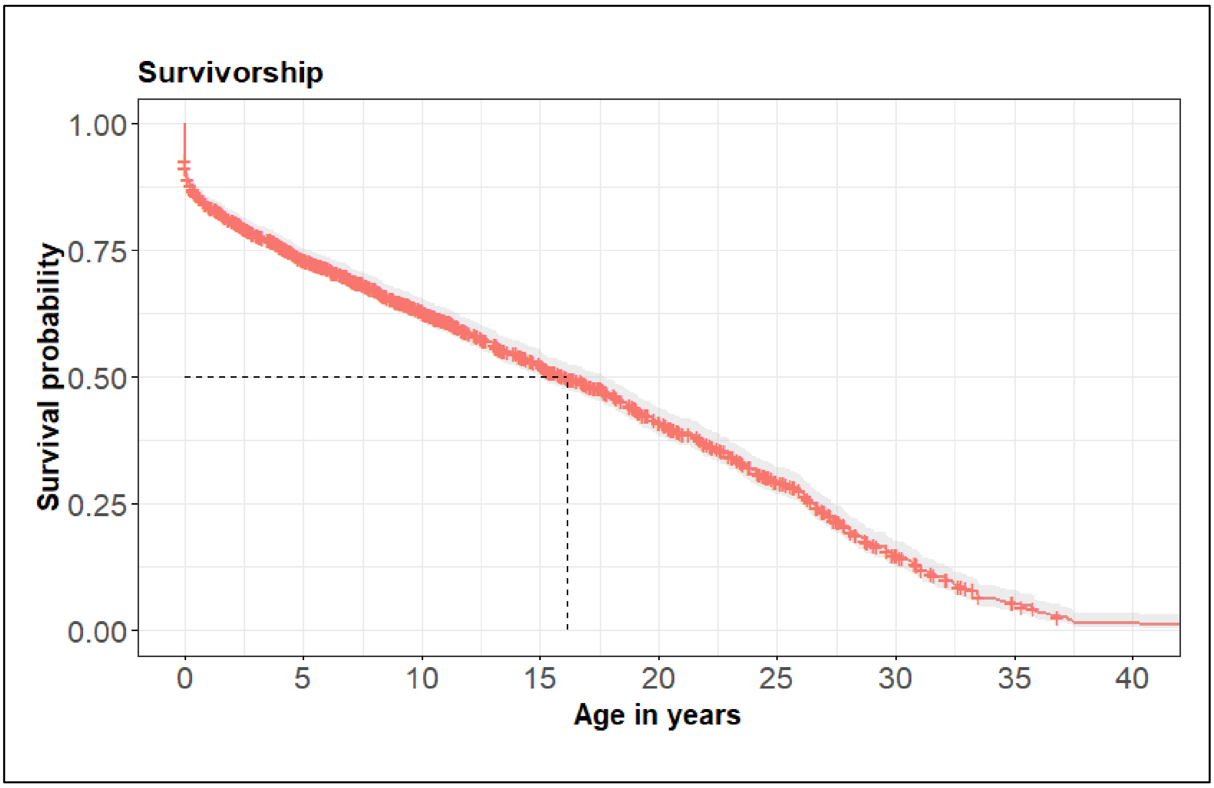


Figure 3. Kaplan-Meier survivorship curve

Patterns of reproduction: reproductive output – females

The global historical population of females was 1,246. Many of them (*c.*60%) never bred. Overall, about 63% (n = 500) of the 800 adult females gave birth at least once in their lifetime. This comprises 40% of the total females. Of the 2,049 infants (with known mothers), 69% (n = 1,421) survived till one year of age. In all, 2,195 infants were born, 146 of them from unidentified mothers.

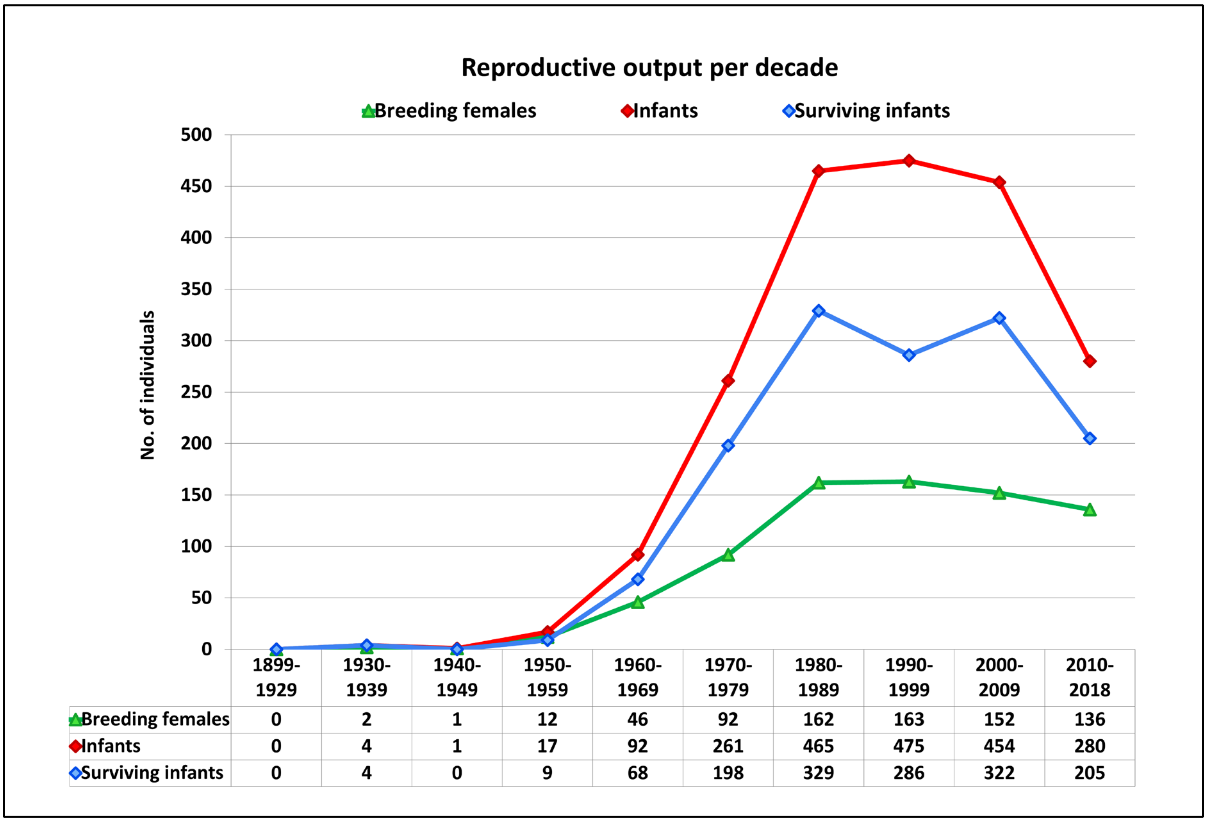
Table 1 provides a breakdown of the contribution of the females to the global captive population. The fact that many females did not give birth at all is reflected in the low number of infants per female, and the breeding females differed considerably in terms of reproductive output. A large proportion of the females (*c.*37.8%) had 1–2 infants, another 38% gave birth to 3–5 infants, 15.6% had 6–8 infants, and 8.6% produced >8 infants each (Table 1). Females also differed considerably with regard to infant survival.

Table 1. Individual reproductive output of the females.

Total females recorded	1,246
Females of minimally 5 years (adult)	800, 64% of total females
Females that bred	500, 40% of total and 63% of adult females
Total infants with known dams	2,049
Mean (± SD) number of infants per female	1.64 ± 2.77
Mean (± SD) number of infants per adult female	2.56 ± 3.11
Mean (± SD) number of infants per breeding female	4.098 ± 3.03
Range of infants per breeding female	1–16
	37.8% of the breeding females produced 1–2 infants, 38% → 3–5 infants, 15.6% → 6–8, 8.6% → >8 infants each
Total infants with known dams that survived till 1 year	1,421
Mean (± SD) number of surviving infants per female	1.14 ± 2.09
Mean (± SD) number of surviving infants per adult female	1.78 ± 2.38
Mean (± SD) number of surviving infants per breeding female	2.84 ± 2.46
Range of surviving infants per breeding female	0–12
	16% of the breeding females did not have a surviving infant, 36% → 1–2, 34% → 3–5, 11% → 6–10, 3% → >8 surviving infants each

Patterns of reproduction: reproductive output over the decades

After a period with small numbers of breeding females in the early decades, the number of females to give birth increased till the end of the 1990s (Fig. 4). Overall, infant mortality remained high (mean 29 ± 6% per decade between 1960 and 2018). The period between 2010 and 2018 showed a strong decrease in the number of breeding females and the number of surviving infants. The total number of breeding females was influenced by birth control measures in North America in the 1990s and in Europe from about 2011 onwards.



	1899-1929	1930-1939	1940-1949	1950-1959	1960-1969	1970-1979	1980-1989	1990-1999	2000-2009	2010-2018
▲Breeding females	0	2	1	12	46	92	162	163	152	136
◆Infants	0	4	1	17	92	261	465	475	454	280
◇Surviving infants	0	4	0	9	68	198	329	286	322	205

Figure 4. Reproductive output of the females per decade

Patterns of reproduction: reproductive output in different locations

One hundred and ninety-two zoos in the global captive population were considered to have the potential to breed (see below chapter "Zoo colonies"). Of these, females in 140 (*c.*73%) of the zoo's were reproducing.

Figure 5a provides an overview of the distribution of adult females over differently sized groups (individuals recorded per location are regarded as a proxy for a group). About 26% of the adult females lived in groups with 2–4 members (median per year), 40% lived in groups with 5–9 members, and 16% lived in groups with 10 or more members. About 18% (n = 147) of the adult females had been transferred between locations of different sizes.

Figure 5b shows the number of breeding females in different group size classes but also provides the number of females that bred in one group size class only. To test for differences in the productivity of the females in the different group size classes, we excluded the females that bred in more than one group size class in order to get independent samples. The Kruskal- Wallis Test revealed that the numbers of infants per breeding female were significantly different between the group size classes (Kruskal-Wallis $\chi^2 = 15.762$, df = 2, p-value <0.001). *Post hoc* pairwise comparisons using the Dunn Test showed that there were significant differences between the small and the larger group size classes (small–medium, p-value = 0.0015; small–large: p-value = 0.0004), and not between the two larger group size classes (medium–large, p-value = 0.3759) (see Fig. 6a). Regarding the number of surviving infants per breeding female, a corresponding difference was also found between the group size classes (Kruskal-Wallis χ^2 = 22.8, df = 2, p-value <0.001), with significant *post hoc* differences occurring between the small and the larger group size classes (Dunn comparison: small–medium, p-value <0.001; small–large, p-value <0.001), and not between the two larger group size classes (medium–large, p-value = 0.12) (see Fig. 6b). The productivity of the females in larger groups (5 and more) is higher. Kept in 66 zoos in all (*c*.34%), they contributed 1,629 infants (*c*.80% of total infants from known dams) (Figs. 5a, 5b). Since birth control was likely to be carried out in locations with larger number of females, the productivity of the latter might be underestimated. Overall, the productivity of the females reveals large differences between the zoos (Fig. 5b).

Most (*c*.84%, n = 102) of the females (n = 121) that produced more than five infants bred in groups with five or more members. The remaining small number of females (*c*.16% of 121) that also produced >5 infants, bred either in groups with 2–4 members (n = 10) or bred in a combination of groups of small and larger sizes (n = 9).

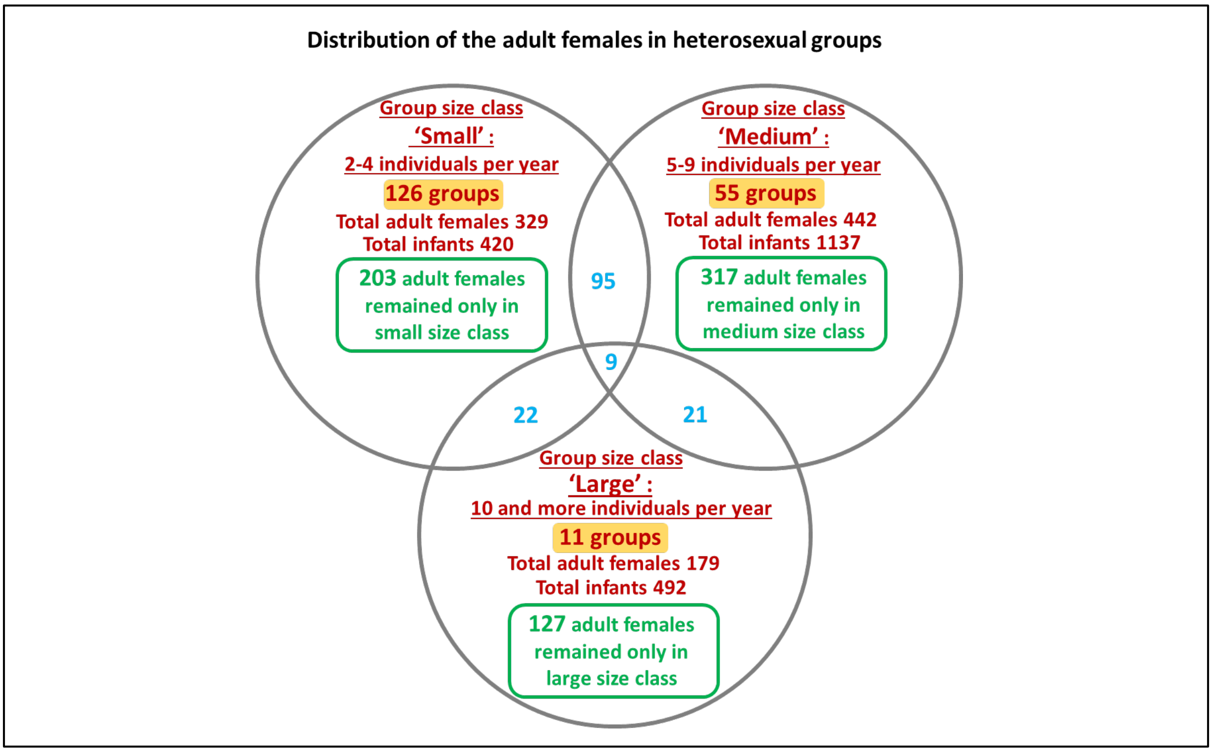


Figure 5a. Distribution of adult females (n = 794) over the three group size classes. Adult females that were transferred and lived in different group size classes (n = 147) are indicated in the overlapping regions of the circles. The females that remained in the same group size class (n = 647) are indicated in the green boxes within the circles.

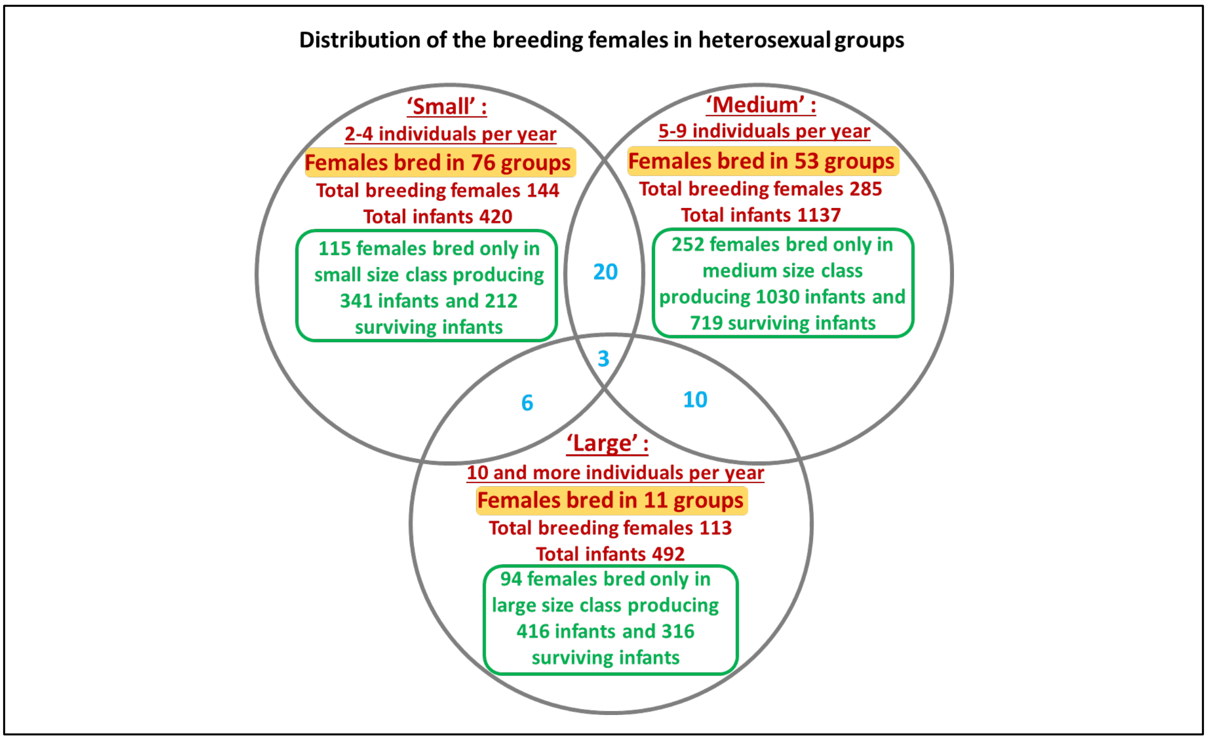


Figure 5b. Distribution and productivity of females that bred in the three group size classes. Females that were transferred and bred in more than one group size class (n = 39) are indicated in overlapping regions of the circles. Females that bred in only the same group size class (n = 461) are indicated in the boxes.

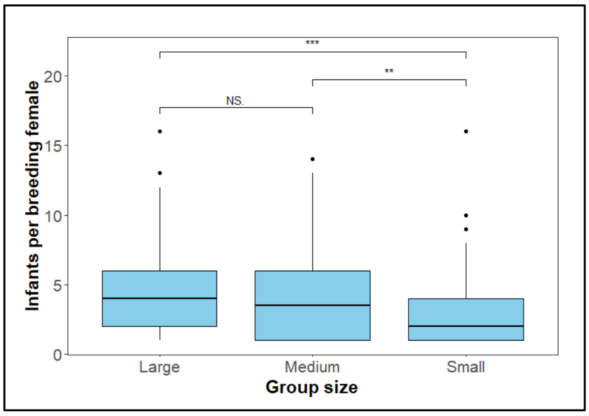


Figure 6a. Infants per breeding female in different group size classes.

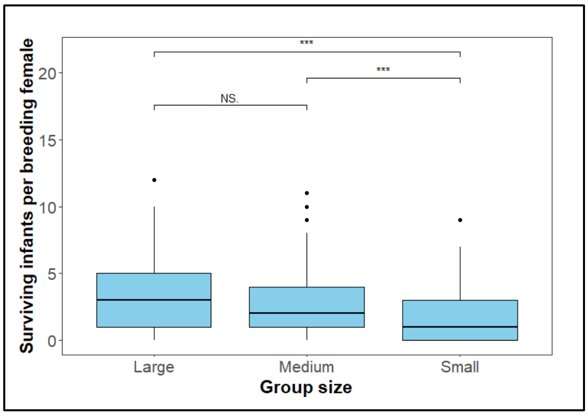


Figure 6b. Surviving infants per breeding female in different group size classes.

*** indicates $p \leq 0.001$, ** indicates $p \leq 0.01$, NS. indicates no significant difference.

Patterns of reproduction: reproductive output of the females in the regions

Table 2a provides an overview on the patterns of reproduction per breeding female in different regions. The breeding females in the two large subpopulations, Europe and North America, produced similar numbers of infants per female (Table 2a). The total number of infants produced was highest in the European subpopulation. In North America, the number of females was reduced because of management decisions (see above). Births there decreased correspondingly.

A number of females (n = 136) were transferred between regions, of which about 14% (n = 19) bred in more than one region. Excluding the latter, i.e., considering only the females that bred in one region (Table 2b), there was no difference in the number of infants per breeding female (Kruskal-Wallis $\chi^2 = 5.9$, df = 4, p-value = 0.20), as well as the number of surviving infants per breeding female (Kruskal-Wallis $\chi^2 = 4.13$, df = 4, p-value = 0.39), between the regions.

The two main regions systematically managed their populations in breeding programs. The North American program started in 1983, and the European one in 1989. Table 3 shows the management periods. For a detailed overview and analysis of the two large populations, see Begum *et al.* (2022).

Since regular breeding has been recorded since 1954 and 1956 in North America and Europe, respectively, the number of infants per adult female are compared from these years onward. The number of infants per adult female in both regions differed between the periods (North America $\chi^2 = 127.05$, p-value < 0.0001; Europe $\chi^2 = 88.99$, p-value <0.0001). In Europe the number was significantly lower prior to the breeding program (without birth control) (Period I–Period II $\chi^2 = 22.88$, p-value <0.0001). In North America, the number of infants per adult female did not differ between the pre-program and breeding program periods without birth control (Period I–Period II $\chi^2 = 3.97$, p-value = 0.14). In both populations, the number differed significantly between program periods with and without birth control. The number of infants per adult female was significantly higher in the program periods without birth control (North America: Period II–Period III $\chi^2 = 89.03$, p-value <0.0001; Europe: Period II–Period III $\chi^2 = 111.21$, p-value <0.0001). In both regions, it was significantly higher in the pre-program period than during the birth control period in the programs (North America: Period I–Period III $\chi^2 = 87.07$, p-value <0.0001; Europe: Period I–Period III $\chi^2 = 27.53$, p-value <0.0001). For further details see Figures 11 and 12 in Begum *et al.* (2022).

Table 2a. Reproductive output of the females per region.

Regions	**Breeding females***	**No. of infants**	**Surviving infants (1 yr.)**	**Mean no. of infants per breeding female**	**Mean no. of surviving infants per breeding female**	**Mean no. of births per female**	**Total no. of females****
North America	156	641	466	4.11±2.92	2.99±2.65	1.62±2.72	395
Europe	240	987	666	4.11±2.96	2.78±2.28	1.68±2.77	588
India	50	161	119	3.22±2.44	2.38±1.85	0.96±1.98	167
Japan	49	189	123	3.86±3.32	2.51±2.51	1.39±2.72	136
Other smaller regions	24	71	47	2.96±2.1	1.96±1.97	0.64±1.55	111

*Table 2a refers to the births and surviving infants from known breeding females. Of the 500 females that bred in captivity, 19 bred in more than one region. **Of the total 1,246 females recorded in the global population, 136 were transferred between regions; including 121 that were recorded in two regions and 15 that were recorded in three regions. For specific regions only, see Table 2b.

Table 2b. Reproductive output of the females breeding in one region only.

Regions	**Females breeding in one region only**	**No. of infants**	**Surviving infants (1 yr.)**	**Mean no. of infants per breeding female (± SD)**	**Mean no. of surviving infants per breeding female (± SD)**
North America	138	563	406	4.08 ± 2.96	2.94 ± 2.66
Europe	229	940	631	4.10 ± 2.95	2.76 ± 2.26
India	49	160	118	3.27 ± 2.44	2.41 ± 1.86
Japan	47	182	120	3.87 ± 3.38	2.55 ± 2.55
Other smaller regions	18	54	35	3 ± 2.25	1.94 ± 2.13

Table 3. Periods in the captive management history of lion-tailed macaques in North American and European zoos.

Management periods	**North America**	**Europe**
(I) Pre-program period with local management only	1899*– 1982	1903*– 1988
(II) Period with breeding program without birth control	1983 – 1989	1989 – 2012
(III) Period with breeding program with birth control	1990 – 2018	2013 – 2018

*First individuals recorded in zoos

Patterns of reproduction: reproductive output – males

The global historical population comprised 1,262 males. Less than 25% (n = 298) of them contributed to reproduction in the population. Between these breeding males, there were large differences in terms of the number of infants. Most breeding males (*c*.54%) produced 1–5 infants, followed by 25% that sired 6–10 infants. A smaller percentage of the breeding males produced more: 11% sired 10–15 infants, 4% sired 16–20, and 6% sired >20 infants each. Few males produced a large proportion of the surviving infants. Table 4 provides details on the contribution of the males to reproduction.

Table 4. Individual reproductive output of the males.

Total males recorded	1,262
Males of minimally 6 years	700, 56% of total males
Males that bred	298, 24% of total and 43% of males of 6 years
Total infants with known sires	2,041
Mean (± SD) number of infants per male	1.62 ± 4.40
Mean (± SD) number of infants per 6-year-old male	2.92 ± 5.57
Mean (± SD) number of infants per breeding male	6.85 ± 6.79
Range of infants per breeding male	1–36
	54% of the breeding males sired 1–5 infants, 25% → 6–10 infants, 11% → 11–15 infants, 4% → 16–20, 6% → >20 infants each
Total infants with known sires that survived till 1 year	1,414
Mean (± SD) number of surviving infants per male	1.12 ± 3.23
Mean (± SD) number of surviving infants per 6-year-old male	2.02 ± 4.11
Mean (± SD) number of surviving infants per breeding male	4.75 ± 5.19
Range of surviving infants per breeding male	0–30
	14% of the breeding males did not have a surviving infant, 56% → 1–5, 19% → 6–10, 5% → 11–15, 4% → 16–20, 2% → >20 surviving infants each

Zoo colonies

Reproductive output of the individual females is undoubtedly influenced by their demographic and social environment. The quality of a captive population as a breeding device is mainly determined by its breeding units (Kaumanns *et al*. 2020). Lion-tailed macaques were kept in 366 zoo colonies over the past 119 years. The size, composition, duration, and environmental conditions of the zoo colonies provide a heterogeneous picture. About 43% (n = 158) of the colonies had only single-sex collections or did not keep both sexes together for more than a year. The composition of heterosexual groups changed over time due to births, deaths, transfers and management decisions. Most of the groups were made up of just a few members (see below).

Quality and size distribution of the groups

The size and consistency of just 53% (n = 192) of the groups had some potential to function as breeding units. To be regarded as such they had to keep individuals of both sexes for at least three years. Many social units in the population were not only small but also suffered from discontinuity. Table 5 provides information about key features of the heterosexual groups and how the various size classes were distributed amongst the zoos. Of the 192 heterosexual groups, 66% (n = 126) had sizes of less than five members per year. The sizes of 29% (n = 55) of the groups ranged between 5 and 9. Only 5% (n = 11) had group sizes of 10 or more. Some zoos, especially zoos with smaller numbers, had periods with single-sex groups or even no groups at all. Groups of more than four members tended to exist for longer (Table 5).

Table 5. Quality of the heterosexual groups.

Group size	**Total zoos**	**Mean (± SD) no. of years with both sexes**	**No. of zoos that sometimes had no animals or had one sex**	**Mean (± SD) no. of years with one sex**	**Mean (± SD) no. of years with no animals**
2 to 4	126	16.9 ± 12.82	103	7.64 ± 8.56	4.87 ± 10.52
5 to 9	55	31.15 ± 17.18	29	3.38 ± 5.14	3.5 ± 10.3
10 and more	11	31.91 ± 19.28	5	2.18 ± 3.09	2.27 ± 7.2
Total	192	21.84 ± 16.04	137	6.10 ± 7.78	4.33 ± 10.28

Using the empirical cumulative distribution function, figures 7 and 8 show the distribution of group sizes in the global historical population and in each region. They are based on the number of individuals in heterosexual groups of two or more members, as registered once at the end of each year from 1907 to 2018. The identity of the groups is not considered. In the global historical captive population, approximately 75% of the heterosexual groups had less than seven members (Fig. 7). About 12% of the groups had 10 or more members. Table 6 shows that in both the large subpopulations, Europe and North America, the conditions were similar (see also Fig. 8). In other subpopulations, group sizes tend to be smaller. Group sizes tended to increase from 1970 onward (Figs. 9 and 10).

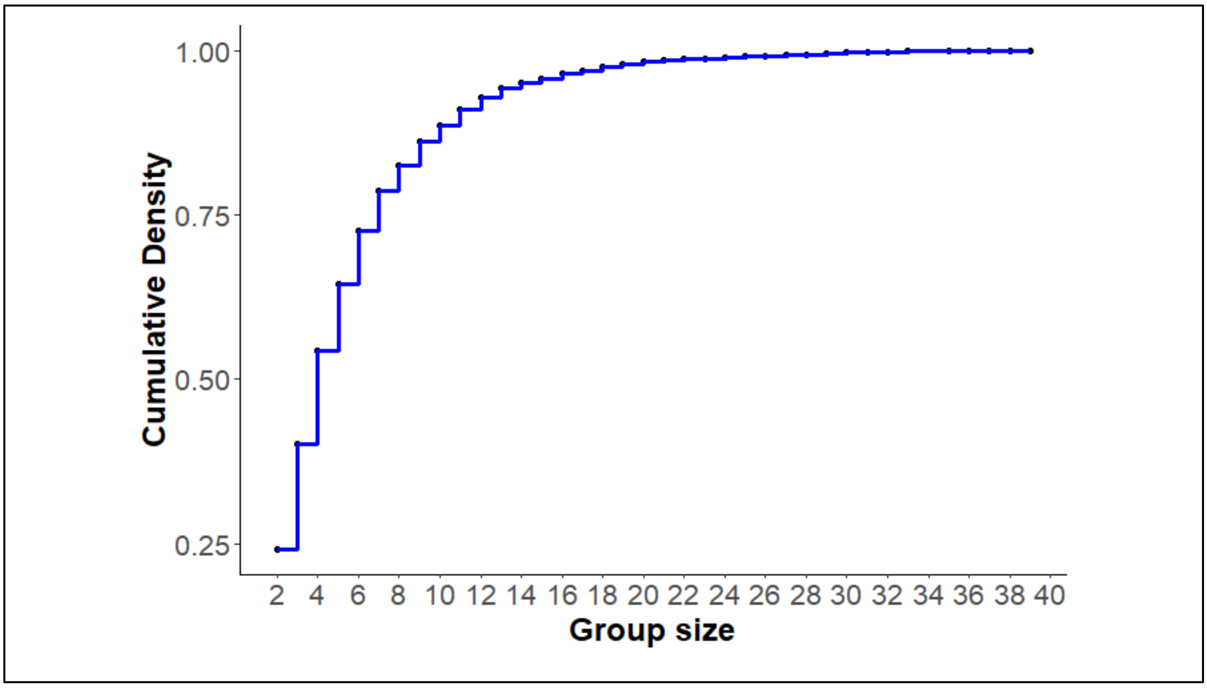


Figure 7. Distribution of sizes of heterosexual groups: Global.

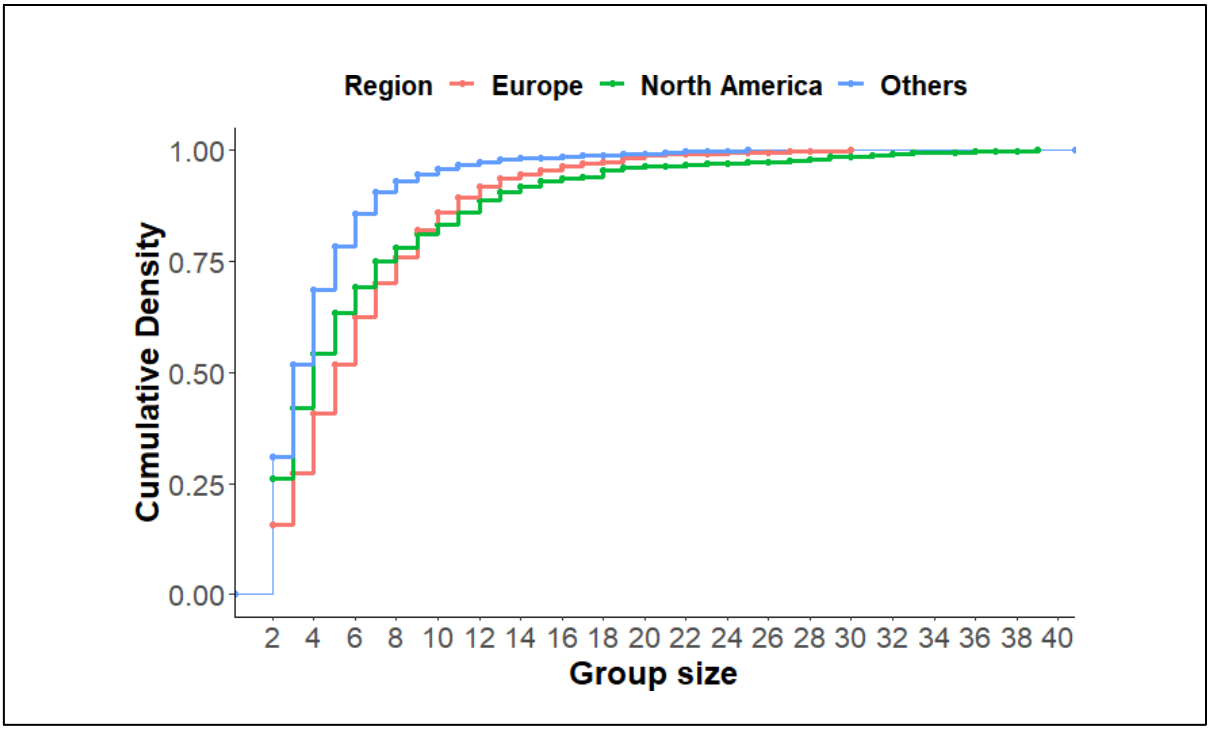


Figure 8. Distribution of sizes of heterosexual groups: Europe, North America, and other regions.

Table 6. Distribution of group sizes in the global historical population and the different regions.

Heterosexual units 1907–2018	Group size			
	Global	Europe	North America	Others
Quantile 75%	7	8	7.5	5
Quantile 50%	4	5	4	3
Range	2 – 39	2 – 30	2 – 39	2 – 25

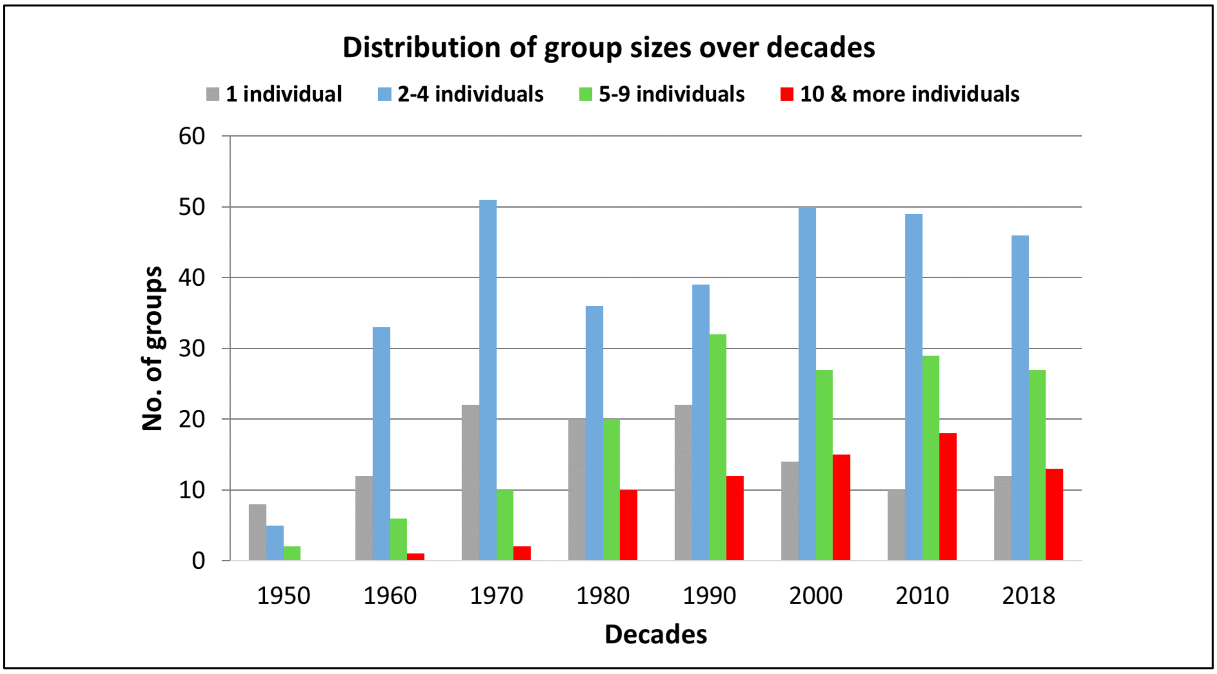


Figure 9. Distribution of different classes of group sizes over decades from 1950 to 2018.

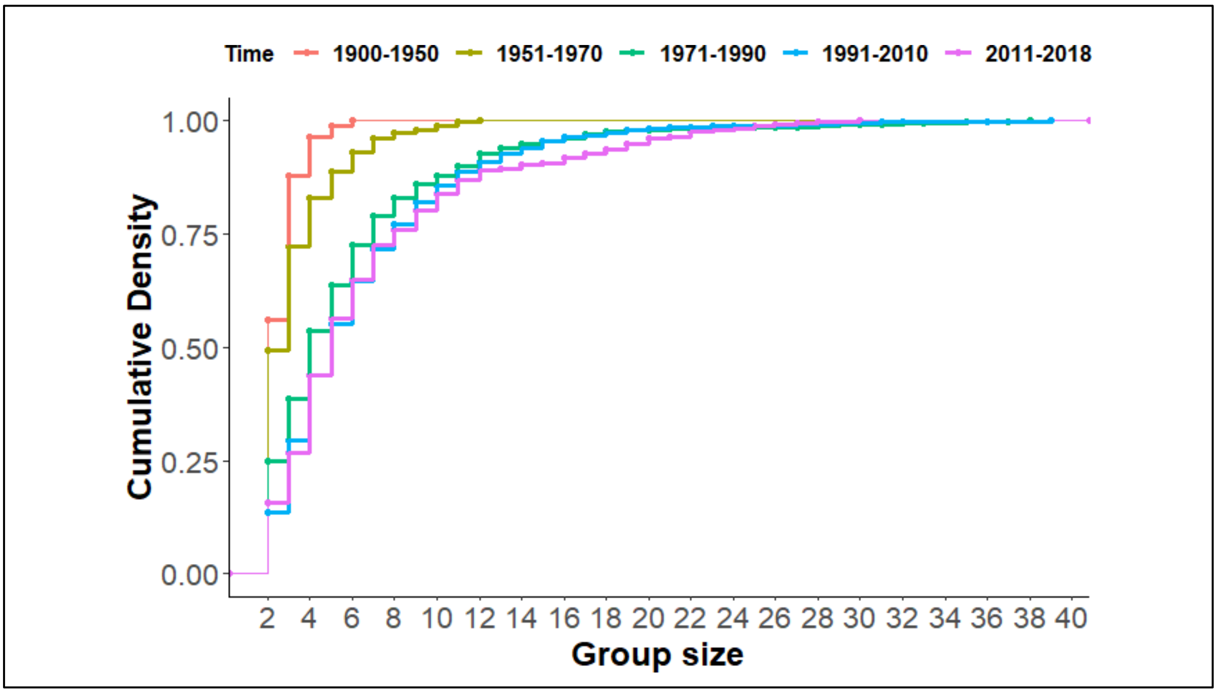


Figure 10. Distribution of group sizes over the years: Global.

Distribution of the number of females in a group in the global population

The number of females (and adult females) in a group is important in the social system of the lion-tailed macaque. Here we describe their numbers in the heterosexual groups, using the empirical cumulative distribution function (Table 7; Figs. 11 and 12). They are based on the number of females in heterosexual groups of two or more members, as registered once at the end of each year. Figure 12 shows the distribution of the number of adult females in the American and European populations during periods when birth control measures were not taken. The number of females (and adult females) kept together was overall small: about 75% of the heterosexual groups had less than four females in the global population (for details see Table 7).

Table 7. Distribution of females in the global historical population and adult females in Europe and North America during non-birth-control period.

Heterosexual units	**Females**	**Adult females**
	Global 1907–2018	**Europe 1989–2006 and North America 1970–1988**
Quantile 75%	4	3
Quantile 50%	2	2
Range	1 – 24	1 – 11

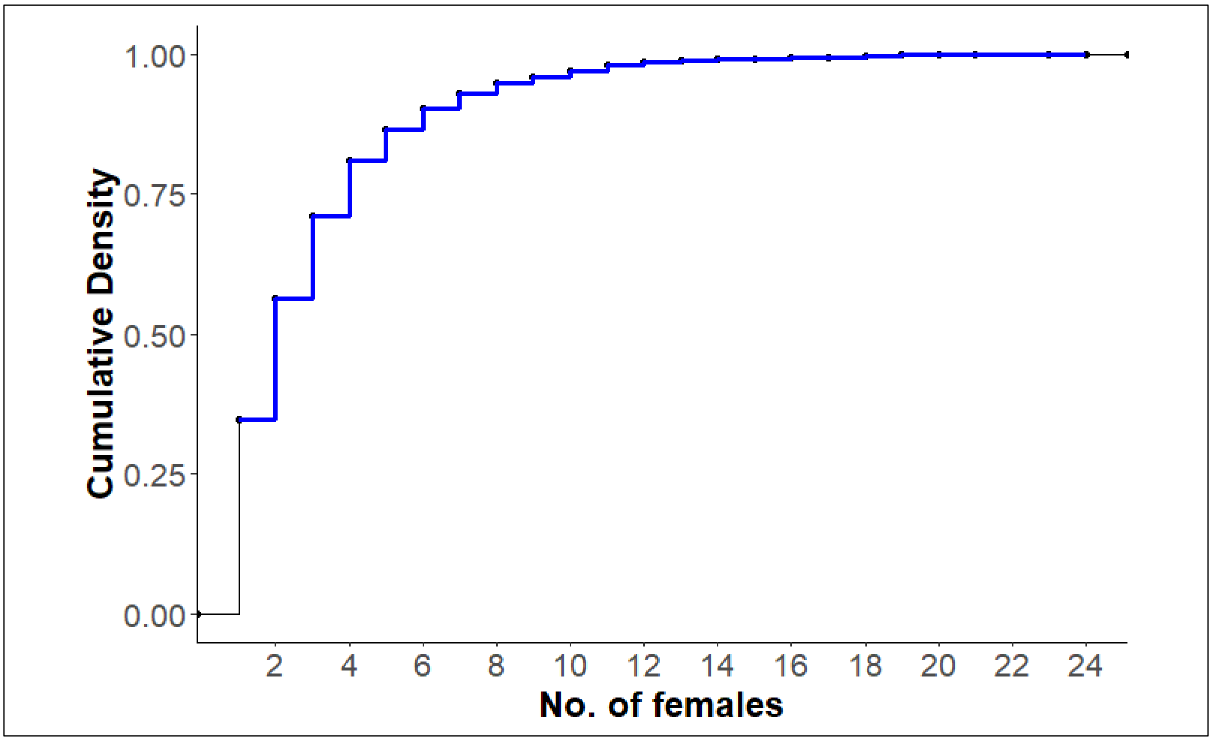


Figure 11. Distribution of the number of females in heterosexual groups from 1907 to 2018: Global.

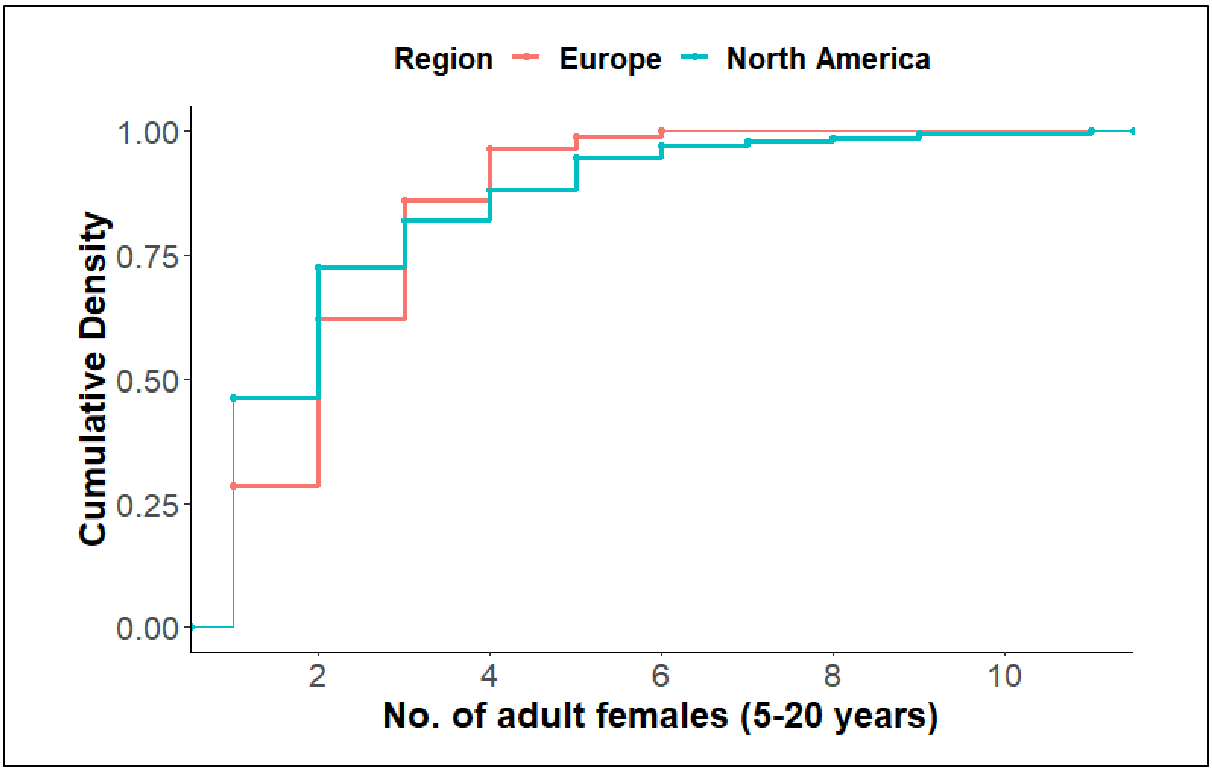


Figure 12. Distribution of the number of adult females in Europe from 1989 to 2006 and North America from 1970 to 1988 in heterosexual groups, during periods without birth control.

Distribution of group sizes in the living population

Being relevant for population management for the living population, groups other than heterosexual ones and singly housed animals are also included (*c.*29%). The distribution of group sizes in the living population is similar to those in the global historical population (Table 8, Figs. 13 and 14). Most group sizes (*c.*75%) are less than 7. The group sizes in Europe are larger than in the other regions.

Table 8. Distribution of group sizes in the global living population as of 2018.

Groups	**Group size**					
	Global (n=98)	**Europe** (n=44)	**India** (n=10)	**Japan** (n=20)	**North America** (n=13	**Others** (n=11)
Quantile 75%	6.75	9	6.5	4.25	3	4.5
Quantile 50%	4	6	2	3.5	2	3
Range	1 – 25	2 – 25	1 – 20	1 – 10	1 – 6	1 – 6

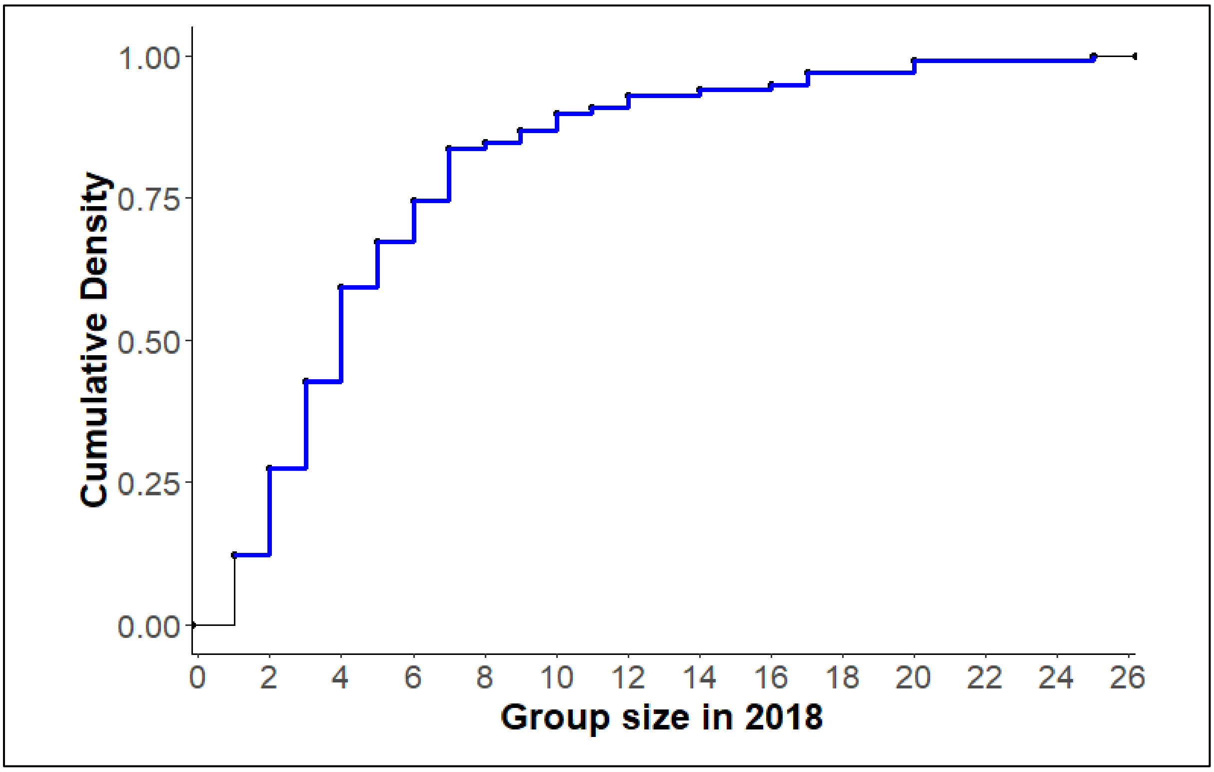


Figure 13. Distribution of group sizes in the current population: Global.

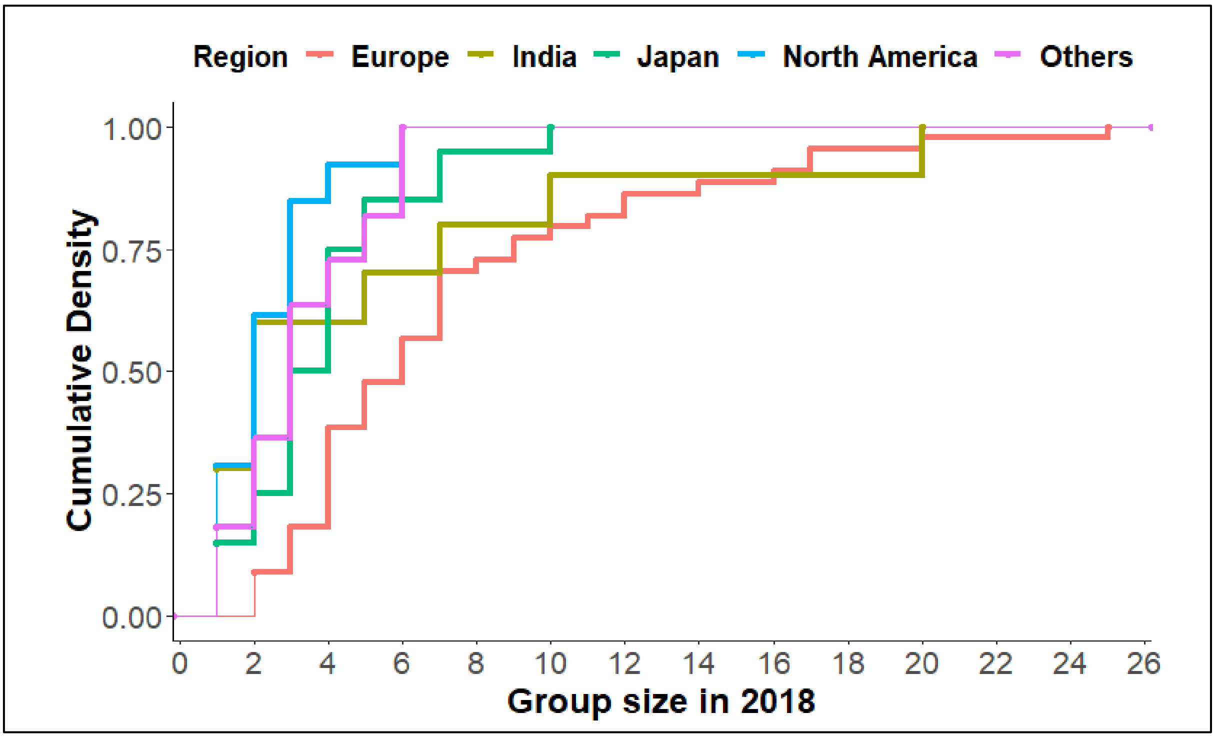


Figure 14. Distribution of group sizes in the current population: Regions.

Management-induced "dispersal": transfers

Up to the 1960s, population development was determined by the import of wild-caught individuals but from then onward, it was influenced by births and deaths. Most zoos in the historical population, after having acquired the "starting set" of lion-tailed macaques either from the wild or from other zoos, occasionally removed or acquired further individuals for their groups. This includes the transfers of 483 captive-born males and 371 captive-born females. Many wild-born females (n = 85) and a few of unknown origin (n = 27), were also transferred to various zoos. A few were transferred between regions (19 wild-born and one of unknown origin females). Population dynamics since the 1960s were strongly influenced by transfers of females between institutions, changing the demographic and social structure of the groups involved.

Global and regional transfers of females

Many of the captive-born females were transferred from their natal groups to other zoos and groups. Figure 15 refers to female transfers from natal groups in the various regions over the decades. It shows that there is a strong increase in transfers between the years 1980 and 2000, and mainly in the North American subpopulation. In the last almost two decades, the number of transfers declined. The number of transfers in the European subpopulation, however, grew slightly and steadily over the last five decades.

Figure 16 provides an overview on the female transfers. It includes information on the ages of the females when transferred from their natal groups. A large proportion (*c.*38%, n = 371) of the captive-born female population (n = 972) was transferred between zoos and lived in more than one location (2–6 locations). About 12% (n = 116) was transferred between regions. About 50% of the captive-born females were transferred as adults and another 50% as infants or juveniles. Infants might have been transferred with their mothers. The frequency of transfers was similar in both North America and Europe.

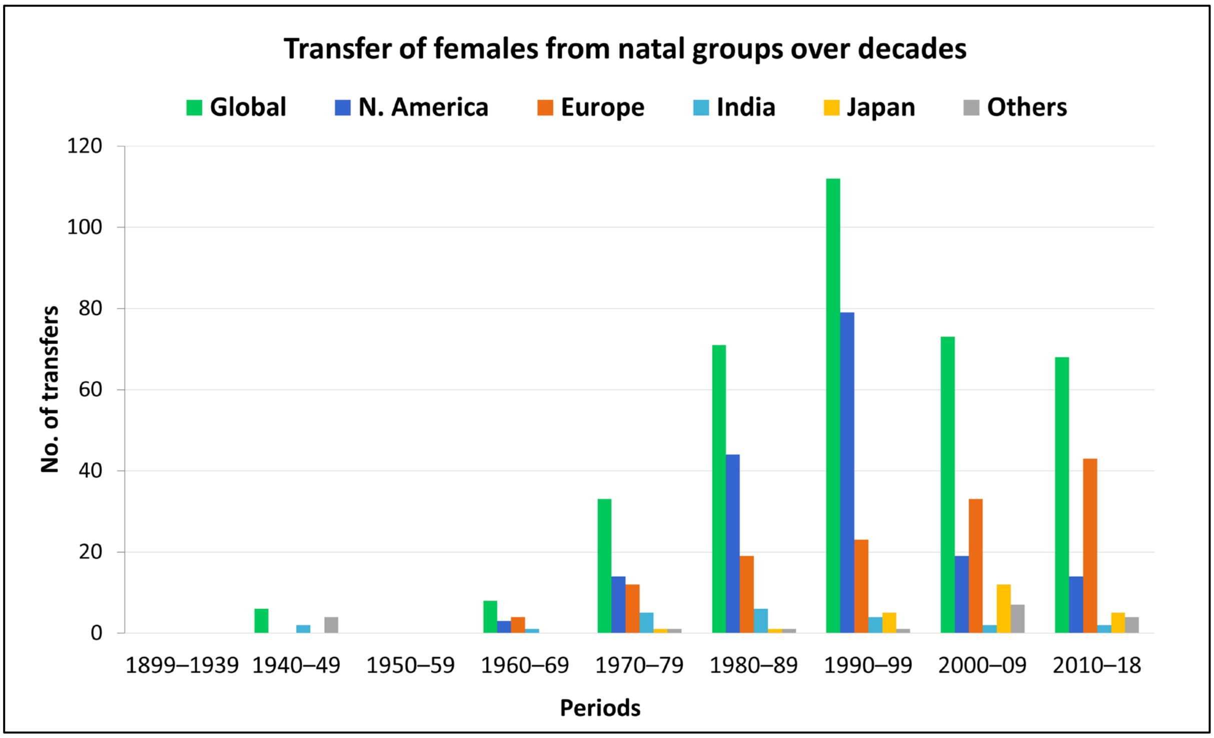


Figure 15. Global and region wise transfer of females from their natal groups over the decades.

Female transfers

Total captive-born females: 972

Total captive-born females transferred from natal groups: 371 (38% of total)

48% of the females transferred were born in North America, **37%** in Europe, **7%** in Japan, **5%** in India and **3%** in other smaller regions

62% (n = 231) of the females were transferred **once**, **23%** (n = 84) **twice**, **11%** (n = 41) **thrice** and **4%** (n = 15) were transferred **4–5 times**

Mean age at transfer from natal group = 6.98 ± 5.64 years

Age at transfer from natal group (years)	No. of transferred females (%)	Region-wise female transfers
< 5	180 (50%)	NA 81, EUR 69, JAP 15, IND 11, OTH 4
5 to 9	88 (24%)	NA 38, EUR 37, JAP 9, IND 3, OTH 1
10 to 14	50 (14%)	NA 26, EUR 13, JAP 3, IND 3, OTH 5
15 and more	45 (12%)	NA 28, EUR 15, IND 1, OTH 1
Total	363*	NA 173, EUR 134, JAP 27, IND 18, OTH 11

*Birth dates were known for 363 out of the 371 transferred females

NA - North America, EUR - Europe, JAP - Japan, IND - India, OTH - Other smaller regions

Figure 16. Female transfers.

Breeding patterns of the females remaining in their natal groups and the transferred females

Of the captive-born females that remained in their natal groups (n = 601), *c*.49% (n = 293), did not survive to the age of 5, thus strongly suppressing the reproductive potential of the population. A few younger females (<5 years) (*c*.5%, n = 29) are alive, and 46% (n = 279) reached adulthood. Of the adult females that remained in their natal groups, 63% (n = 175) bred and produced 651 infants. Several adult females (n = 105) bred in their natal groups before they were transferred to new groups. In all, natal group females gave birth to 1,013 infants, 46% of the total (n = 2,195) born into the population. Considering captive-born mothers only (n = 408), 59% (n = 1,013) of the infants (n = 1,716) were born in the natal group of the mothers.

Forty-six percent (n = 170) of the females that were transferred bred in the new groups. They constitute about 52% of the transferred females that reached adulthood. Seven-hundred and three infants were born to females transferred from their natal groups. They account for 41% of the infants produced by captive-born mothers, and 32% of all infants born into the population.

The Wilcoxon Rank Sum Test was used to compare the reproductive output of adult captive-born females in natal (n = 279) and non-natal groups (n = 272). For this analysis, we excluded the females that reproduced in both natal and non-natal groups (n = 42). The females that bred in natal groups before transfer (n = 63) but did not breed in the new groups have been excluded from the sample of females in natal groups. Females that were transferred at the age of 20 years or more (n = 11) were excluded from the sample of females in non-natal groups. The resulting sample comprised 279 adult females in natal groups and 272 adult females in non-natal groups. They produced 651 and 527 infants in natal and non-natal groups, respectively.

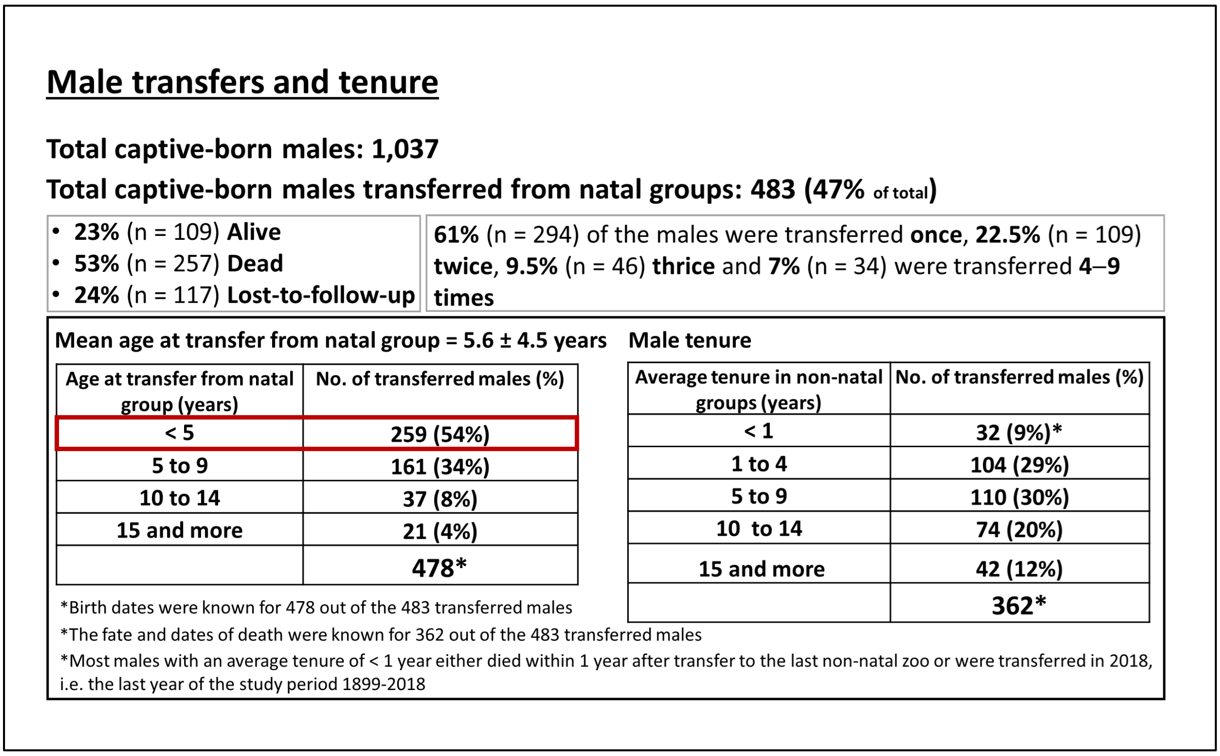
The number of infants per adult female was significantly higher in natal groups (2.33 ± 2.91 infants per female) than in non-natal groups (1.94 ± 2.76 infants per female) (Wilcoxon Rank Sum Test, W = 33369, p = 0.01). The number of surviving infants per adult female was also significantly higher in natal groups (1.53 ± 2.03 infants per female) than in non-natal groups (1.34 ± 2.17 infants per female) (Wilcoxon Rank Sum Test, W = 33768, p = 0.01).

Overall, 32.5% (n = 196) of adult captive-born females did not breed at all. The reproductive output of the adult females remaining in their natal groups was significantly higher than the output of the females that were transferred to new groups.

Transfer and tenure of males

Figure 17 provides an overview of the transfer of males between zoos and their tenure in a group. About 50% of the captive-born males of the historical population were transferred from their natal groups. About 62% of the transferred males remained in the corresponding new locations for more than 5 years.

Fifty-four percent of the males that were transferred were less than five years old. A large proportion (*c.*59%, n = 283) of the males transferred did not breed. Overall, more than 75% (n = 964) of the total males did not breed at all (see above).



Male transfers and tenure

Total captive-born males: 1,037

Total captive-born males transferred from natal groups: 483 (47% of total)

- **23%** (n = 109) **Alive**
- **53%** (n = 257) **Dead**
- **24%** (n = 117) **Lost-to-follow-up**

61% (n = 294) of the males were transferred **once**, **22.5%** (n = 109) **twice**, **9.5%** (n = 46) **thrice** and **7%** (n = 34) were transferred **4–9 times**

Mean age at transfer from natal group = 5.6 ± 4.5 years

Age at transfer from natal group (years)	No. of transferred males (%)
< 5	259 (54%)
5 to 9	161 (34%)
10 to 14	37 (8%)
15 and more	21 (4%)
	478*

Male tenure

Average tenure in non-natal groups (years)	No. of transferred males (%)
< 1	32 (9%)*
1 to 4	104 (29%)
5 to 9	110 (30%)
10 to 14	74 (20%)
15 and more	42 (12%)
	362*

*Birth dates were known for 478 out of the 483 transferred males

*The fate and dates of death were known for 362 out of the 483 transferred males

*Most males with an average tenure of < 1 year either died within 1 year after transfer to the last non-natal zoo or were transferred in 2018, i.e. the last year of the study period 1899-2018

Figure 17. Male transfers and tenure.

Discussion

Overview

The lion-tailed macaque is endangered in its natural habitat (Singh *et al*. 2020) as well as in captivity (see Singh *et al.* 2009; Sliwa and Begum 2019). Our investigation focused on the patterns of reproduction in the global historical captive population of the lion-tailed macaque, which indicated reasons for its low productivity. Corresponding data are rarely available for other primates and our analysis could well serve as a model. The aim of breeding programs is to achieve the long-term persistence of the captive population but information on the potential problems and management implications resulting from the long-term perspective are often lacking (see Lindburg 2001; Begum *et al.* 2022). The sustainability of captive populations is currently one of the key topics of zoo biology (Lees and Wilcken 2009; Leus *et al*. 2011; Powell *et al*. 2019).

We expected that the productivity of the population would be low. From the distribution of group sizes with overall small numbers of individuals per location, we concluded that most individuals of the population were living under demographic and the resulting social conditions that established mismatches with species-typical adaptations: a large proportion of the females did not breed at all. Infant mortality was high, forming a large proportion of overall mortality (for details see Begum *et al.* 2022). This patterning characterizes the population over its full history (see also Lindburg 1980; Kaumanns and Rohrhuber 1995; Kaumanns *et al*. 2013). Population development was influenced by birth control measures on a large scale, adding to the low productivity.

Throughout the existence of the population, groups deviated demographically from those typical in the wild. Most of the captive groups had less than five members. The (social) stability of the groups was impeded by the removal and transfer of females between institutions and groups on a large scale (see also Lindburg and Lasley 1985). In the wild, females usually remain in their natal groups lifelong. The life of captive lion-tailed macaques in small, unstable groups does not match the species-typical social way of living in female-bonded larger groups in the wild. Following the concepts of life history theory, this may result in low productivity at the population level (see Stearns 2000; Kaumanns and Singh 2015; Kaumanns *et al.* 2020).

Patterns of reproduction

Less than 50% of the females in the global historical captive population contributed to successful breeding, and individual differences were large. Similar patterns are not reported from wild groups or subpopulations in contiguous undisturbed forests. In their comprehensive review of the reproductive biology of the lion-tailed macaque, Singh *et al*. (2006a) concluded that an average female in the wild may contribute up to about five infants during a reproductive span of about 15 years in her lifetime, but this low number is compensated with the relatively high survivorship of infants and seems to keep the size of the population close to carrying capacity. Infant survivorship rate in the wild ranges from 0.80 to 0.973 (Kumar 1995; Sharma 2002; Krishna *et al.* 2006; see also Singh *et al.* 2006a). Although infants are born throughout the year (Krishna *et al*. 2006), two breeding peaks are observed in the wild (Sharma *et al.* 2006). In captivity, lion-tailed macaques breed throughout the year (Lindburg *et al.* 1989; Krebs and Kaumanns 2001). According to Kumar (1987), Singh *et al.* (2006a, 2009) and Singh (2019), some of the life history patterns of the lion-tailed macaque result in a slow turnover between the generations and can make small subpopulations prone to a rapid decline after catastrophic events such as extreme food shortage or increased unnatural deaths of even a few individuals in areas of high human disturbance (Kumara *et al.* 2000; Singh *et al.* 2001) or due to hunting (see Kumara and Sinha 2009).

Of the females in the captive population that bred, a small number produced more than five infants and a larger number less than five. Females that remained in their natal groups produced more infants than those that were transferred. Considering the large number of females without offspring, our findings reveal an overall low productivity at the population level, as also reported by Lindburg *et al.* (1989), Kaumanns and Rohrhuber (1995), Krebs and Kaumanns (2001) and Singh *et al.* (2006a).

A low number of (surviving) infants per adult female is regarded as the most critical feature of the historical captive population of the lion-tailed macaque. Low productivity in this sense is likely to induce vulnerability for “breakdowns” in a population, corresponding to catastrophic events in the wild. In captivity, breakdowns may be induced by invasive management measures, such as large-scale birth control and the removal or loss of individuals due to infectious diseases, in a large proportion of the population. The development of the North American subpopulation serves as an example for risks (for details see Begum *et al.* 2022). Birth control measures on a large scale contributed to the decline of the population. In the early period without management programs and in the period without birth control during management, the number of infants per adult female was significantly higher.

Despite low productivity, the population revealed a slow but steady growth from the 1960s onward to 2018 via births into the population and without further integration of wild-caught individuals (Begum *et al.* 2022). This positive trend does not imply, however, development toward a secure population status. Our study indicates maladaptive patterns of reproduction that can hinder the persistence of the population in the long run and result in a further loss of genotypic and phenotypic diversity.

Features indicating mismatches: groups

Most collections lived in groups that deviated demographically from those typical in the wild. Most of them had less than five members with few adult females. Groups in large contiguous forests tend to have a modal group size of 16–21, consisting of an adult male, a number of adult females, and immature individuals (for example, Kumar 1987; Ramachandran and Joseph 2000; Kumara and Singh 2004; Kumara *et al.* 2014; Sushma *et al.* 2014; Singh 2019). Groups in forest fragments can be small or large, ranging from seven to 90 individuals (Singh *et al.* 2002; Umapathy and Kumar 2000; Umapathy *et al.* 2011). Life in small groups does not match with the natural social environment of lion-tailed macaques that provides conditions for the realization of species-typical traits.

Low productivity might be influenced by the small group sizes that do not match with demographic and social requirements of the reproductive system of lion-tailed macaques. This assumption is supported by additional hints on the importance of group size for productivity: females in larger groups contributed a larger proportion of the infants. Females in the many small groups contribute little. It seems inappropriate, however, to conclude that the size of the large groups *per se* is the critical feature. Typically, larger groups existed over decades and experienced fewer management-induced changes. Overall, they probably provided better conditions to realize the species-typical features of the social system. It is likely, however, that in the larger groups birth control has been executed occasionally for space reasons, concealing the 'real' productivity of the females. The value of the large groups as the most productive units in the population might be underestimated.

A minimal number of group members is possibly a necessary but not a sufficient condition for the optimal functioning of the reproductive system of the species. Since social behavior is significantly influenced by demographic parameters, variance in group size may affect behavior and reproduction (Singh and Kaumanns 2005). With reference to the female-bonded system of lion-tailed macaques, the number and age-structure of the females in a group might be of special importance.

Features indicating mismatches: transfers

The social stability of groups in the population was often impeded by the removal of females from natal groups and their subsequent introduction into new groups. Transfers of some individuals were carried out frequently and sometimes repeatedly. Females of all age classes were transferred. Transfers are not compatible with the female-bonded social structure (see also Lindburg *et al.* 1997). The transfers executed on a large scale produced "dispersal patterns" of the females that are not found in the wild—another mismatch that might influence productivity negatively. Adult females that were transferred from their natal group to other groups had fewer infants.

In the wild, the splitting of large groups can occasionally lead to the establishment of new groups (Umapathy *et al*. 2011; G. Umapathy pers. comm. June 2022). Kaumanns *et al*. (2006) recommended, therefore, following this pattern of splitting large groups along matrilines for the establishment of new groups in captive conditions.

Contrary to female dispersal, male dispersal is an integral part of the social system and population dynamics in wild lion-tailed macaques (see Kumar *et al.* 2001). The males in the historical captive population were transferred on a large scale. The transfers included individuals of all ages, with a large proportion (*c*.41%) of males younger than four years, as infants and early juveniles. The removal of juvenile males is likely to have negative consequences for their behavioral development (see also Lindburg 1992). Many males remained in non-natal groups for many years. It is likely, that the tenure of adult males in wild groups is shorter. It corresponds to a higher interest of females in "new" males migrating into groups (see Kumar *et al*. 2001; see also Harvey and Lindburg 2001). Overall, however, the fate of the many transferred males remained unclear. It is likely, that many of them had to live under suboptimal conditions since only a small number of breeding males was needed and adult males are not compatible in unisex groups (see Lindburg 2001; Kaumanns *et al.* 2006; Kaumanns and Singh 2012).

Features indicating mismatches: fragmentation

Over the more than 100 years of its existence in hundreds of zoos, the captive population of the lion-tailed macaque was highly fragmented. This influenced its development and the patterns of reproduction (see Kaumanns *et al.* 2008). With small group sizes, a low and variable number of infants per female, the patterns of reproduction and demographic structures as found in the present study might be similar to the ones found in wild groups in forest fragments (see also Singh and Kaumanns 2005; Kaumanns *et al*. 2008). In most of the latter, the birth rate was lower than that in more contiguous forests (Kumar *et al.* 1995). Reproductive output in lion-tailed macaque groups in small fragments is lower than in large fragments (Umapathy and Kumar 2000, 2003). Singh (2019) noted that lion-tailed macaques in forest fragments overall have more variable density, demography, and birth rates than in large forest expanses. Dispersal of males might also be hindered in forest fragments (Umapathy and Kumar 2000) and might lead to longer tenures of the males in the groups. It is evident that isolated groups of lion-tailed macaques in captivity and in fragmented natural habitats are likely to experience mismatches with reference to species-typical dispersal patterns and a lack of group encounters (see Kaumanns *et al*. 1998; Zinner *et al*. 2001). The latter can play an important role for mate-choice processes in the context of male migration to other groups and the acceptance of a new male by the resident females (Kumar and Kurup 1985; Kaumanns *et al*. 1998; Kumar *et al*. 2001).

Considering the altered demographic structures in the historical population, it is likely that Allee effects (Allee 1931; Courchamp *et al.* 2008; Swaisgood and Schulte 2010) contributed to breeding problems and low population growth—low numbers of offspring induce conditions that again led to low numbers in the next generation.

Consequences of mismatches: social relationships

From their small size and poor demographic structure, it has to be concluded that most captive groups did not cover several generations, and their, often management-induced, small and constant size would be unfavorable for the establishment of clans of related females that stay lifelong in their natal groups. This social network is an adaptation and key-trait of the social system of lion-tailed macaques and of several other macaque species ("female-bonded system") (see Thierry *et al.* 2004), and therefore could not be realized in most social units of the captive population. It is likely that atypical demographic structures, and in particular the small sizes of the groups in the historical population, induce social problems for the group members, and that the "management" of social relationships, especially of conflicts, is impeded. Wild lion-tailed macaque females interact in hierarchical structures within and between clans (Singh *et al.* 2006b). They also compete for access to males (Kumar 1987; Sharma 2002). Related females support each other, and affiliative behaviors are more common between members of the same matriline (see Birky 1993; Zaunmair *et al.* 2015, for female social relationships in captive groups). Their social life in the wild is embedded in long-term familiarity (see Thierry *et al.* 2004) and is realized via extended spacing patterns (see Jeyraj 2003; Singh *et al.* 2010) in the higher strata of the evergreen mountainous forests the species inhabits. Group members forage individually and are often widely dispersed (Sushma 2004). Enclosures in zoos rarely allow for the realization of a normal social life under such conditions (Kaumanns *et al*. 2006, 2008).

It is likely, that the discrepancies and mismatches described, and a life in the reduced zoo environment, contribute to the emergence of welfare problems and the development of inappropriate socialization conditions for young lion-tailed macaques. They might hinder the development of social competence, especially with reference to infant rearing in the females (see Lindburg and Fitch-Snyder 1994). The so-far-unexplained low productivity including high infant mortality that has characterized the population over most of its history might result from a lack of competence and skills in the mothers (see Kaumanns *et al.* 2008, 2013) and also the males (see Lindburg and Lasley 1985; Lindburg *et al*. 1989, 1997). Concluding from studbook data, many individuals grew up without siblings and with only a few old group mates (see also Lindburg 1992). Rox *et al*. (2022) found that reproductive output in captive rhesus macaques kept in multigenerational groups was higher than those kept in peer groups.

Potential consequences of mismatches: life histories

It seems likely that the set of life histories and the resulting life-history patterns in a population, especially concerning individual reproductive behavior, supported maladaptive population structures and fitness problems. According to life-history theory much of what happens in a population and influences reproductive success is fitness relevant (see Roff 1992; Stearns 1992, 2000; Daan and Tinbergen 1997). Social life evolved toward permanent strong bonds between the females—a key trait of the lion-tailed macaque (as in related species; see Thierry *et al*. 2004). The management and husbandry of the global historical population over long time periods failed to provide optimal living conditions, with resulting negative consequences for life histories, notably breeding problems. A large proportion of non-breeding females can threaten the persistence of a population. From life-history theory, it is deduced that fitness-relevant traits should guide population management. We propose to consider the female-bonded social system of the lion-tailed macaque as a fitness relevant system and propagate a better integration into the captive propagation of the species (see also Kaumanns *et al.* 2006, 2020; Kaumanns and Singh 2015).

Other potential reasons for low productivity and breeding problems

A retrospective study by Penfold *et al.* (2014) has shown that extended periods of non-breeding can have negative consequences for the reproductive system of the females and for their breeding potential in a captive population. We detected non-breeding periods in individuals, groups, and subpopulations, the negative consequences of which have been demonstrated in such as African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) (Hildebrandt *et al.* 2000; Hermes *et al.* 2004), white rhinoceroses (*Ceratotherium simum*) (Hermes *et al.* 2006) and cheetahs (*Acinonyx jubatus*) (Wachter *et al.* 2011; Ludwig *et al.* 2019). Carter and Ness (2012) pointed to problems with inducing breeding in captive lion-tailed macaques after periods of non-breeding.

Reports on the patterns of reproduction in fragmented wild groups of lion-tailed macaques and the results of this study on the groups of the fragmented captive population both indicate that the reproductive system of the species is sensitive to alterations in demography, social conditions, and dynamics. Key traits (see Carroll and Watters 2008) such as life in female-bonded structures are of critical importance for local and overall persistence (Kaumanns *et al.* 2020). Our studies on the global historical captive population of the lion-tailed macaque provide a "magnifying perspective" on the effects of alterations under more extreme conditions than currently found in the wild. Conservation management in the fragmented wild population might also have to strongly emphasize aspects of the reproductive system of lion-tailed macaques (see also Singh *et al.* 2006a). This would include preventing the complete isolation of groups through the establishment of corridors and canopy bridges, and transfer of non-related males (see Kumar *et al.* 2001; Singh *et al.* 2002, 2009; Umapathy *et al.* 2011; Singh 2019). If possible, living conditions in forest fragments should be improved to allow for larger groups.

Conclusions

Our analysis indicates a large waste and loss of phenotypic and genetic diversity due to the large proportion of females that did not breed successfully. The mismatches and the highly fragmented structure in time and space of the global population were evidently influenced by a broad spectrum of management decisions, different environmental conditions, and husbandry systems that produced proximate conditions finally leading to the modest and labile current status (see Sliwa and Begum 2019; Begum *et al.* 2021). Local management prior to the breeding programs was likely to be suboptimal: important traits of the lion-tailed macaque were not known in the earlier decades (Lindburg and Lasley 1985; Lindburg *et al.* 1989). Components of the systematic management carried out later in the North American breeding program were biased toward genetic aspects and neglected the fact that the phenotype as a whole has to be the unit of management (Kaumanns *et al.* 2013; Kaumanns and Singh 2015). A captive population with a history over many decades is inevitably influenced by different managers and their management approaches, both locally and globally (see Lindburg 2001) and can suffer from periods of inappropriate management. It has to remain open, however, for and integrate new developments regarding the biology of the species and other relevant aspects. This should be an integral part of the breeding programs and should be institutionalized internationally and follow the principles of adaptive management (see Walters and Hilborn 1978). In its first twenty years, the population of the European breeding program for instance was managed correspondingly with close *in situ – ex situ* cooperation. It supported the persistence of the global population after the loss of the American subpopulation. Adaptive management is of special importance with reference to the management of population size via birth control as often considered in dealing with space problems in zoos (see also Begum *et al.* 2022).

Significant improvements in the management of the captive population of the lion-tailed macaque are required since the poor status of the wild population (see Singh *et al.* 2020) still indicates the need for an *ex situ* reserve population (see Singh *et al.* 2009, 2012, 2020; Begum *et al.* 2021). A future management plan for the captive lion-tailed macaque population should integrate the results of our studbook analysis (see also Begum *et al.* 2022). As a key aspect, we propose appropriate social management via the establishment of species-typical groups of female-bonded social units, as was suggested in the European breeding program (Kaumanns *et al.* 2013). Our study revealed maladaptive developments in the patterns of reproduction in the historical but also current captive population. Management should aim at preserving the reproductive potential of the population (see Kaumanns *et al.* 2020). The majority of the females should be able to breed in species-typical patterns and predictively. Since more corresponding know-how is needed, it is necessary to establish relevant applied research projects following the "declining population paradigm" as elaborated by Caughley (1994). Concepts of evolutionary biology and conservation biology dealing with the adaptive potential of a species must be considered (see Kaumanns and Singh 2015; Schulte-Hostedde and Mastromonaco 2015; Kaumanns *et al.* 2020). A new management approach should be preceded by the development of a long-term perspective for the global captive population of the lion-tailed macaque. For details, see Begum *et al.* (2021, 2022).

With reference to the limited information as provided by our studbook data, this study has used a mainly descriptive approach. It intends to provide the materials to learn from the past for the future management of the threatened study population and other captive and wild primate populations. The results from a sample of thousands of lion-tailed macaques kept in hundreds of zoos over a hundred years has a validity that allows conclusions supporting more successful conservation-oriented management.

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Literature Cited

Allee, W. C. 1931. *Animal Aggregations: A Study in General Sociology.* University of Chicago Press, Chicago, IL.

Ballou, J. D., R. C. Lacy and J. P. Pollak. 2020. PMx: Software for Demographic and Genetic Analysis and Management of Pedigreed Populations (Version 1.6.2.20200110). Chicago Zoological Society, Brookfield, IL. Website: <http://www.scti.tools>. Accessed 30 August 2020.

Begum, N., W. Kaumanns, A. Sliwa and M. Singh. 2021. The captive population of the lion-tailed macaque *Macaca silenus*. The future of an endangered primate under human care. *J. Threat. Taxa* 13(9): 19352–19357.

Begum, N., W. Kaumanns, M. Singh and H. Hofer. 2022. Hundred years in zoos: history and development of the captive population of the lion-tailed macaque *Macaca silenus.* Long term persistence for conservation? *Primate Conserv.* (36): 155–172.

Birky, W. A. 1993. Female-female Social Relationships in a Captive Group of Lion-Tailed Macaques (*Macaca silenus*). MSc thesis, California State University, Northridge, CA.

Candolin, U. and B. B. M. Wong. (eds). 2012. *Behavioural Responses to a Changing World. Mechanisms and Consequences.* Oxford University Press, Oxford, UK.

Carroll, S. P. and J. V. Watters. 2008. Managing phenotypic variability with genetic and environmental heterogeneity: contemporary evolution as a first principle of conservation biology. In: *Conservation Biology-Evolution in Action,* S. P. Carroll and C. W. Fox (eds.), pp.181–198. Oxford University Press, Oxford, UK.

Carter, S. and T. Ness. 2012. Population Analysis & Breeding and Transfer Plan Lion-tailed Macaque (*Macaca silenus*) AZA Species Survival Plan Yellow Program. Minnesota Zoo, MN, and Association of Zoos and Aquariums (AZA), Silver Spring, MD. 28pp.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* 63(2): 215–244.

Clutton-Brock, T. H. and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.* 25(10): 562–573.

Conway, W. 1985. Saving the lion-tailed macaque. In: *The Lion-tailed Macaque: Status and Conservation,* P. G. Heltne (ed.), pp.1–12. Alan R Liss, New York.

Courchamp, F., L. Berec and J. Gascoigne. 2008. *Allee Effects in Ecology and Conservation*. Oxford University Press, Oxford, UK.

Daan, S. and J. M. Tinbergen. 1997. Adaptations and life histories. In: *Behavioural Ecology: An Evolutionary Approach*. 4th edition, J. R. Krebs and N. B. Davies, (eds.), pp.311–333. Blackwell Science, Oxford, UK.

Fitch-Snyder, H. 2006. *International Lion-tailed Macaque Archive Studbook Macaca silenus*. San Diego Zoo, San Diego, CA.

Harvey, N. C. and D. G. Lindburg. 2001. A long-term decline in swelling of the sexual skin in captive lion-tailed macaques. *Primate Rep.* 59: 43–49.

Heltne, P. G. (ed.). 1985. *The Lion-tailed Macaque: Status and Conservation.* Alan R. Liss, Inc., New York.

Hendry, A. P. *et al.* 2011. Evolutionary principles and their practical application. *Evol. Appl.* 4(2): 159–183.

Hermes, R., T. B. Hildebrandt and F. Göritz. 2004. Reproductive problems directly attributable to long-term captivity-asymmetric reproductive aging. *Anim. Reprod. Sci.* 82–83: 49–60.

Hermes, R. *et al*. 2006. The effect of long non-reproductive periods on the genital health in captive female white rhinoceroses (*Ceratotherium simum simum, C. s. cottoni*). *Theriogenology* 65(8): 1492–1515.

Hildebrandt, T. B., F. Göritz, N. C. Pratt, J. L. Brown, R. J. Montali, D. L. Schmitt, G. Fritsch and R. Hermes. 2000. Ultrasonography of the urogenital tract in elephants (*Loxodonta africana* and *Elephas maximus*): an important tool for assessing female reproductive function. *Zoo Biol.* 19(5): 321–332.

Jeyraj, T. 2003. A Study of Male Behavior in Lion-tailed Macaques (*Macaca silenus*) with Special Reference to Male-Male Interactions. MSc thesis, University of Mysore, Mysore, India.

Kaplan, E. L. and P. Meier. 1958. Nonparametric estimation from incomplete observations. *J. Am. Stat. Assoc.* 53(282): 457–481.

Kaumanns, W. and B. Rohrhuber. 1995. Captive propagation in lion-tailed macaques: the status of the European population and research implications. In: *Research and Captive Propagation,* U. Gansloßer, J. K. Hodges and W. Kaumanns (eds.), pp.296–309. Filander Verlag, Fürth.

Kaumanns, W. and M. Singh. 2012. Social relationships among lion-tailed macaques (*Macaca silenus*) in differently structured social units. *Curr. Sci.* 102(10): 1451–1455.

Kaumanns, W. and M. Singh. 2015. Towards more individual-based and fitness-oriented captive mammal population management. *Curr. Sci.* 109(6): 1121–1129

Kaumanns, W., D. Zinner, and J. Hindahl. 1998. Experimentelle Gruppenbegegnungen als Mittel zur sozialen Stimulans bei in Menschenhand gehaltenen Bartaffen (*Macaca silenus*). *Zool. Garten* 68 (1): 45–55.

Kaumanns, W., C. Schwitzer, P. Schmidt and C. Knogge. 2001. The European lion-tailed macaque population: an overview. *Primate Rep.* 59: 65–76.

Kaumanns, W., E. Krebs and M. Singh. 2006. An endangered species in captivity: husbandry and management of the lion-tailed macaque (*Macaca silenus*). *MyScience* 1(1): 43–71.

Kaumanns, W., M. Singh and C. Schwitzer. 2008. Primate populations in zoos: a case of fragmentation. *Primate Rep.* 76: 41–54.

Kaumanns, W., M. Singh and A. Sliwa. 2013. Captive propagation of threatened primates – the example of the lion-tailed macaque *Macaca silenus*. *J. Threat. Taxa* 5(14): 4825–4839.

Kaumanns, W., N. Begum and H. Hofer. 2020. "Animals are designed for breeding": captive population management needs a new perspective. *J. Zoo Aquar. Res.* 8(2): 76–85.

Kempske, S. 1985. *Macaca silenus*: survey of North American and European zoo practices. In: *The Lion-tailed Macaque: Status and Conservation,* P. G. Heltne (ed.), pp.221–235. Alan R. Liss Inc., New York.

Krebs, E. and W. Kaumanns. 2001. *European Studbook for the Lion Tailed Macaque* (*Macaca silenus*). Zoologischer Garten Köln, Köln, Germany.

Krishna, B. A., M. Singh and M. Singh. 2006. Population dynamics of a group of lion-tailed macaques (*Macaca silenus*) inhabiting a rainforest fragment in the Western Ghats, India. *Folia Primatol.* 77(5): 377–386.

Kumar, A. 1987. The Ecology and Population Dynamics of Lion-tailed Monkeys (*Macaca silenus*) in South India. PhD thesis, Cambridge University, Cambridge, UK.

Kumar, A. 1995. Birth rate and survival in relation to group size in the lion-tailed macaques. *Primates* 36(1): 1–9.

Kumar, A. and G. U. Kurup. 1985. Inter-troop interactions in the lion-tailed macaque *Macaca silenus*. In: *The Lion-tailed Macaque: Status and Conservation*, P. G. Heltne (ed.), pp.91–107. Alan R. Liss, Inc., New York.

Kumar, A., G. Umapathy and A. Prabhakar. 1995. A study on the management and conservation of the small mammals in fragmented rainforests of Western Ghats, south India: a preliminary report. *Primate Conserv.* (16): 53–58.

Kumar, M. A., M. Singh, H. N. Kumara, A. K. Sharma and C. Bertsch. 2001. Male migration in lion-tailed macaques. *Primate Rep.* 59: 5–18.

Kumara, H. N. and M. Singh. 2004. Distribution and abundance of primates in rainforests of the Western Ghats, Karnataka, India and the conservation of *Macaca silenus*. *Int. J. Primatol.* 25(5): 1001–1018.

Kumara, H. N. and A. Sinha 2009. Decline of the endangered lion-tailed macaque, *Macaca silenus*, in the Western Ghats, India. *Oryx* 43(2): 292–298.

Kumara, H. N., A. K. Sharma, M. A. Kumar and M. Singh. 2000. Roadkills of wild fauna in Indira Gandhi Wildlife Sanctuary, Western Ghats, India: implications for management. *Biosphere Conserv.* 3(1): 41–47.

Kumara, H. N., R. Sasi, R. Suganthasakthivel, M. Singh, H. S. Sushma, K. K. Ramachandran and W. Kaumanns. 2014. Distribution, demography, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anamalai Hills landscape, Western Ghats, India. *Int. J. Primatol.* 35(5): 976–989.

Lees, C. M. and J. Wilcken. 2009. Sustaining the ark: the challenges faced by zoos in maintaining viable populations. *Int. Zoo Yearb.* 43(1): 6–18.

Leus, K., L. B. Lackey, W. van Lint, D. De Man, S. Riewalt, A. Veltkam and J. Wijmans. 2011. Sustainability of European Association of Zoos and Aquaria bird and mammal populations. *WAZA Mag.* 12: 11–14.

Lindburg, D. G. 1980. Status and captive reproduction of the lion-tailed macaque *Macaca silenus*. *Int. Zoo Yearb.* 20(1): 60–64.

Lindburg, D. G. 1992. Group size for captive lion-tailed macaques. *Lion-Tales* 8(1–2): 4–5.

Lindburg, D. G. 2001. A century of involvement with lion-tailed macaques in North America. *Primate Rep.* 59: 51–64.

Lindburg, D. G. and H. Fitch-Snyder. 1994. Use of behavior to evaluate reproductive problems in captive mammals. *Zoo Biol.* 13(5): 433–445.

Lindburg, D. G. and K. A. Forney. 1992. Long-term studies of captive lion-tailed macaques. *Primate Rep.* 32: 133–142.

Lindburg, D. G. and L. Gledhill. 1992. Captive breeding and conservation of lion-tailed macaques. *Endang. Species Update* 10(1): 1–4.

Lindburg, D. G. and B. L. Lasley. 1985. Strategies for optimizing reproductive potential of lion-tailed macaque colonies in captivity. In: *The Lion-tailed Macaque: Status and Conservation,* P. G. Heltne (ed.), pp. 343–356. Alan R. Liss, Inc., New York.

Lindburg, D. G., A. M. Lyles and N. M. Czekala. 1989. Status and reproductive potential of lion-tailed macaques in captivity. *Zoo Biol. Suppl.* 1: 5–16.

Lindburg, D. G., J. Iaderosa and L. Gledhill. 1997. Steady-state propagation of captive lion-tailed macaques in North American zoos: a conservation strategy. In: *Primate Conservation: The Role of Zoological Parks*, J. Wallis (ed.), pp.131–149. Special Topics in Primatology, Volume 1. American Society of Primatologists, Chicago, IL.

Ludwig, C., M. Dehnhard, S. Pribbenow, S. Silinski-Mehr, H. Hofer and B. Wachter. 2019. Asymmetric reproductive aging in cheetah (*Acinonyx jubatus*) females in European zoos. *J. Zoo Aquar. Res.* 7(2): 87–93.

Mason, G., C. C. Burn, J. A. Dallaire, J. Kroshko, H. McDonald Kinkaid and J. M. Jeschke. 2013. Plastic animals in cages: behavioural flexibility and responses to captivity. *Anim. Behav.* 85(5): 1113–1126.

Nuss, K. and M. Warneke. 2010. Life span, reproductive output, and reproductive opportunity in captive Goeldi's monkeys (*Callimico goeldii*). *Zoo Biol.* 29(1): 1–15.

Penfold, L. M., D. M. Powell, K. Traylor-Holzer and C. S. Asa. 2014. "Use it or lose it": characterization, implications, and mitigation of female infertility in captive wildlife. *Zoo Biol.* 33(1): 20–28.

Powell, D. M., C. L. Dorsey and L. J. Faust. 2019. Advancing the science behind animal program sustainability: an overview of the special issue. *Zoo Biol.* 38(1): 5–11.

Princée, F. P. G. 2016. *Exploring Studbooks for Wildlife Management and Conservation.* Topics in Biodiversity and Conservation. Springer Nature, Cham, Switzerland.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website: <https://www.R-project.org/>. Accessed 24 March 2022.

Ramachandran, K. K. and G. K. Joseph. 2000. Habitat utilization of lion-tailed macaque (*Macaca silenus*) in Silent Valley National Park, Kerala, India. *Primate Rep.* 58: 17–25.

Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York, USA.

Rox, A., S. Waasdorp, E. H. M. Sterck, J. A. M. Langermans and A. L. Louwerse. 2022. Multigenerational social housing and group-rearing enhance female reproductive success in captive rhesus macaques (*Macaca mulatta*). *Biology* 11(7): 970.

Schulte-Hostedde, A. I. and G. F. Mastromonaco. 2015. Integrating evolution in the management of captive zoo populations. *Evol. Appl.* 8(5): 413–422.

Scobie, P and L. Bingaman Lackey. 2012. Single Population Analysis and Records Keeping System (SPARKS) (Version 1.66). International Species Information System (ISIS, renamed to Species360). Eagan, MN, USA.

Sharma, A. K. 2002. A Study of the Reproductive Behaviour of Lion Tailed Macaque (*Macaca silenus*) in the Rainforests of Western Ghats. PhD thesis, University of Mysore, Mysore.

Sharma, A. K., M. Singh, W. Kaumanns, E. Krebs, M. Singh, M. A. Kumar and H. N. Kumara. 2006. Birth patterns in wild and captive Lion-tailed Macaques (*Macaca silenus*). *Int. J. Primatol.* 27(5): 1429–1439.

Sheldon, B. C., L. E. B. Kruuk and S. C. Alberts. 2022. The expanding value of long-term studies of individuals in the wild. *Nat. Ecol. Evol.* 6(12): 1799–1801.

Sih, A. 2013. Understanding variation in behavioural responses to human induced rapid environmental change: a conceptual overview. *Anim. Behav.* 85(5): 1077–1088.

Sih, A., M. C. O. Ferrari and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* 4(2): 367–387.

Singh, M. 2019. Management of forest-dwelling and urban species: case studies of the lion-tailed macaque (*Macaca silenus*) and the bonnet macaque (*M. radiata*). *Int. J. Primatol.* 40(6): 613–629.

Singh, M. and W. Kaumanns. 2005. Behavioural studies: a necessity for wildlife management. *Curr. Sci.* 89(7): 1230–1236.

Singh, M., H. N. Kumara, M. A. Kumar and A. K. Sharma. 2001. Behavioural responses of lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rain forest fragment in the Western Ghats, India. *Folia Primatol.* 72(5): 278–291.

Singh, M., M. Singh, M. A. Kumar, H. N. Kumara, A. K. Sharma and W. Kaumanns. 2002. Distribution, population structure, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anaimalai Hills, Western Ghats, India. *Am. J. Primatol.* 57(2): 91–102.

Singh, M., A. K. Sharma, E. Krebs and W. Kaumanns. 2006a. Reproductive biology of lion-tailed macaque (*Macaca silenus*): an important key to the conservation of an endangered species. *Curr. Sci.* 90(6): 804–811.

Singh, M., B. A. Krishna and M. Singh. 2006b. Dominance hierarchy and social grooming in female Lion-tailed Macaques (*Macaca silenus*) in the Western Ghats, India. *J. Biosci.* 31(3): 369–377.

Singh, M., W. Kaumanns, M. Singh, H. S. Sushma and S. Molur. 2009. The lion-tailed macaque *Macaca silenus* (Primates: Cercopithecidae): conservation history and status of a flagship species of the tropical rainforests of the Western Ghats, India. *J. Threat. Taxa* 1(3): 151–157.

Singh, M., T. Jeyaraj, U. Prashanth and W. Kaumanns. 2010. Male–male relationships in lion-tailed macaques (*Macaca silenus*) and bonnet macaques (*Macaca radiata*). *Int. J. Primatol.* 32(1): 166–176.

Singh, M., W. Kaumanns and G. Umapathy. 2012. Conservation-oriented captive breeding of primates in India: is there a perspective? *Curr. Sci.* 103(12): 1399–1400.

Singh, M., A. Kumar and H. N. Kumara. 2020. *Macaca silenus*. The IUCN Red List of Threatened Species 2020: e.T12559A17951402. <http://www.iucnredlist.org>. Accessed 16 July 2021.

Sliwa, A. and N. Begum. 2019. *International Studbook 2018 for the Lion-tailed Macaque Macaca silenus Linnaeus, 1758, Edition 2018 – Volume 9.* Zoologischer Garten Köln, Köln, Germany.

Sliwa, A., K. Schad and E. Fienig. 2016. Long-term Management Plan for the Lion tailed macaque (*Macaca silenus*) European Endangered Species Programme (EEP). Zoologischer Garten Köln, Köln, Germany and European Association of Zoos and Aquaria (EAZA), Amsterdam, Netherlands. 60pp.

Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.

Stearns. S. C. 2000. Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* 87(11): 476–486.

Sushma, H. S. 2004. Resource utilization and niche separation in sympatric rainforest arboreal mammals. PhD thesis, University of Mysore, Mysore, India.

Sushma, H. S., R. Mann, H. N. Kumara and A. Udhayan. 2014. Population status of the endangered lion-tailed macaque *Macaca silenus* in Kalakad-Mundanthurai Tiger Reserve, Western Ghats, India. *Primate Conserv.* (28): 171–178.

Swaisgood, R. R. and B. A. Schulte. 2010. Applying knowledge of mammalian social organization, mating systems and communication to management. In: *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* 2nd Edition, D. G. Kleiman, K. Thompson and C. Kirk Baer (eds.), pp.329–343. The University of Chicago Press, Chicago, IL.

Therneau, T. 2022. A Package for Survival Analysis in R. R Package Version 3.3-1. Website: <https://CRAN.R-project.org/package=survival>. Accessed 3 July 2022.

Thierry, B., M. Singh and W. Kaumanns. (eds.). 2004. *Macaque Societies: A Model for the Study of Social Organization.* Cambridge University Press, Cambridge, UK.

Umapathy, G. and A. Kumar. 2000. The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Anamalai Hills, south India. *Primates* 41(2): 119–126.

Umapathy, G. and A. Kumar. 2003. Impacts of forest fragmentation on lion-tailed macaque and Nilgiri langur in Western Ghats, south India. In: *Primates in Fragments: Ecology and Conservation*, L. K. Marsh (ed.), pp.163–189. Kluwer Academic/Plenum Press, New York.

Umapathy, G., S. Hussain and S. Shivaji. 2011. Impact of habitat fragmentation on the demography of lion-tailed macaque (*Macaca silenus*) populations in the rainforests of Anamalai Hills, Western Ghats, India. *Int. J. Primatol.* 32(4): 889–900.

Wachter, B., S. Thalwitzer, H. Hofer, J. Lonzer, T. B. Hildebrandt and R. Hermes. 2011. Reproductive history and absence of predators are important determinants of reproductive fitness: the cheetah controversy revisited. *Conserv. Lett.* 4(1): 47–54.

Walters, C. J. and R. Hilborn. 1978. Ecological optimization and adaptive management. *Ann. Rev. Ecol. Evol. Syst.* 9(1): 157–188.

Zaunmair, P., M. Mangalam, W. Kaumanns, M. Singh and L. Slotta-Bachmayr. 2015. Patterns of dominance relationships among the females of a captive female-only group of lion-tailed macaques (*Macaca silenus*) during the course of the introduction of a new adult male. *Curr. Sci.* 109(4): 803–807.

Zinner, D., J. Hindahl and W. Kaumanns. 2001. Experimental intergroup encounters in lion-tailed macaques (*Macaca silenus*). *Primate Rep.* 59: 77–92.

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The Captive Population of the Lion-tailed Macaque *Macaca silenus* (Linnaeus, 1758). The Future of an Endangered Primate under Human Care

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Contributions of the authors

Nilofer Begum and Werner Kaumanns developed the concept and organisation of the manuscript. Alexander Sliwa contributed to its structure under the perspective of the international studbook keeper and EEP Coordinator for the lion-tailed macaque. Mewa Singh commented under the perspective of *in situ* – *ex situ* links and cooperation.

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VIEWPOINT

The captive population of the Lion-tailed Macaque *Macaca silenus* (Linnaeus, 1758). The future of an endangered primate under human care

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Abstract: For conservation breeding, the endangered Lion-tailed Macaques have been maintained in North America under SSP since 1983 and in Europe under EEP since 1989. Based on a growing interest to support the species long-term survival, the SSP population increased considerably during the first few years of the programme but due to space problems and resulting birth control measures, it has drastically declined to small numbers and a non- breeding status at present. The EEP population continually increased till 2012, but due to the lack of spaces and birth control practises, it has gradually declined since then. It is emphasised that the knowledge gained from field studies on Lion-tailed Macaques in India and its incorporation for captive management under EEP has helped develop appropriate management strategies. Captive propagation of the Lion-tailed Macaque in India, the habitat country, can profit from the successes and drawbacks of the long-term management experiences of SSP and EEP.

Keywords: Captive breeding, SSP, EEP, Indian captive population, meta population management.

For most of its history, the captive population of the Lion-tailed Macaque (LTM) was mainly constituted by the North American and the European subpopulations and by a number of other small subpopulations (e.g., India and Japan). Figure 1 and Figure 2 provide an overview on its development, births, imports, and losses. They, like other data used for this paper, are based on the last edition of the international studbook for the LTM (Sliwa & Begum 2019). The North American breeding programme (Species Survival Plan, SSP) for the LTM was established in 1983 with 163 individuals in about 30 zoos (Gledhill 1985). The European programme (European Endangered Species Programme, EEP) was established in 1989, comprising 89 individuals in 12 institutions. Currently, the latter comprises 322 individuals in 44 institutions. The EEP was coordinated by Dr. Werner Kaumanns (German Primate Center; since 2000 curator of primates at Cologne Zoo) till his retirement in 2006. Dr. Alexander Sliwa, Cologne Zoo, is the coordinator since then. The European population grew slowly but steadily to a size of 338 individuals in 2012 but decreased to a current size of 322 individuals in 2018 (Figure 1). The number of births decreased drastically since 2011 (global- Figure 2, European- Figure 3, for more information see below). The American SSP population with its first coordinator and (International)

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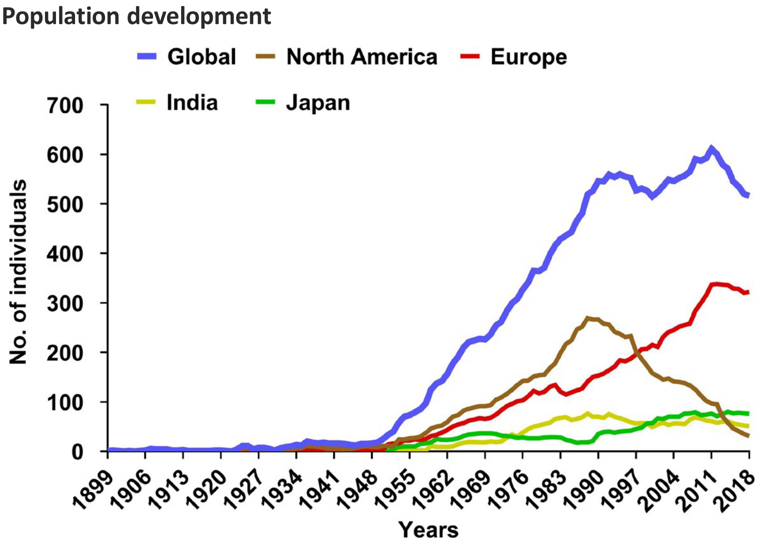

Figure 1. Development of the global historical population.

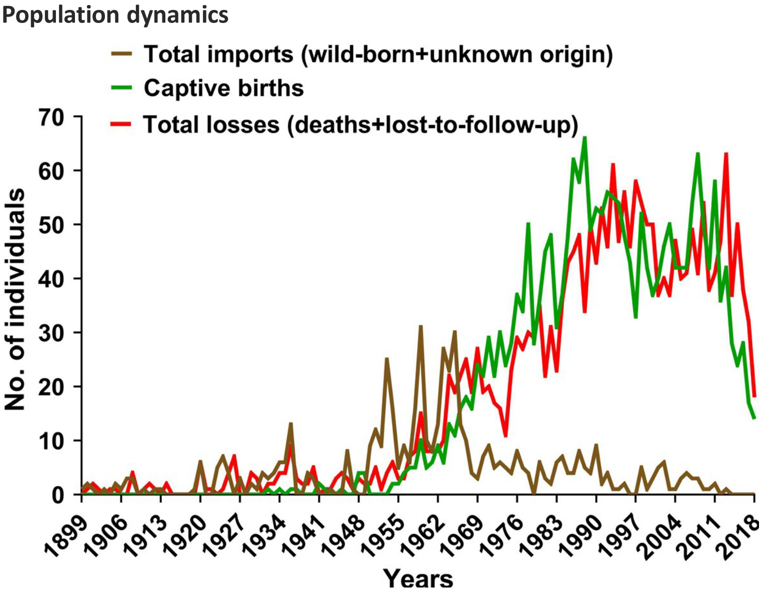

Figure 2. Annual number of imports, births and losses in the global historical population

studbook keeper Laurence Gledhill had its peak size and productivity in the decade after the start of the SSP, with about 269 individuals in 1988. Currently, there are only 31 individuals living (Sarno 2018). The reasons for the decrease were space problems, widely executed birth control measures in the 1990s, ageing, and possibly loss of interest (Lindburg 2001; Ness 2011, 2013). The Indian captive population currently comprises 51 individuals including 16 wild-born macaques. The Japanese Lion-tailed Macaque subpopulation has 76 individuals; other smaller stocks comprise 36 individuals totally.

The current global population comprises 516 individuals in 98 zoos. The wild population of the LTM at present is estimated to be about 4,000 individuals, distributed in 47 isolated subpopulations at seven locations (Singh et al. 2020), with less than 2,500 mature individuals in about 200 groups. The current captive population in 98 groups, therefore, constitutes about 11% of the global population.

The breeding programmes for the LTM always acted with a perspective on the species in the wild. The establishment of the SSP for the LTM was realised assuming that at that time only about 1,000 LTMs were left in the wild (see Hill 1971). To establish a

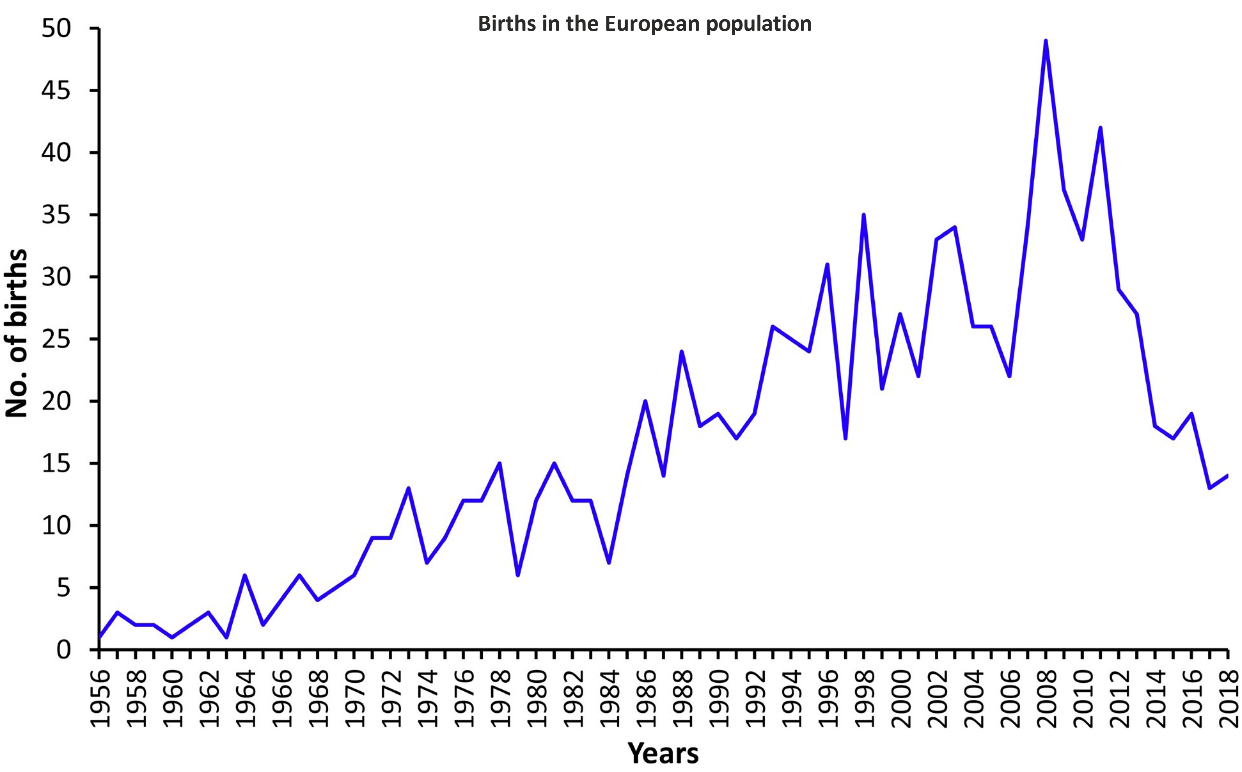

Figure 3. Annual number of births in the European population.

reserve in zoos was intended. Contacts and cooperation between American and Indian institutions were realised (including financial support for field studies). American scientists and especially Dr. Donald Lindburg, San Diego Zoological Society, contributed important studies both with reference to the biology of the species and its captive propagation (e.g., Lindburg et al. 1989; Lindburg & Gledhill 1992; Lindburg & Harvey 1996).

Almost since its establishment, the European LTM population was managed in contact with Indian wildlife biologists. Results from their studies on the wild population in its natural habitat (Western Ghats, southern India) were integrated. Since 1998 (till 2004) the annual reports for the captive population also reported on the status and other relevant aspects of the wild population. This was based on a close (ongoing) cooperation of the first EEP coordinator with Dr. Mewa Singh and Dr. Ajith Kumar. Prof. Mewa Singh, University Mysore, leading Indian primatologist, and wildlife biologist visited Germany to work on LTM matters with Dr. Werner Kaumanns since the 1990s more than 25 times. Mainly due to Mewa Singh and his working group, the conservation of the LTM became and is still an important issue in India. In addition to grants from major Indian sources, some of the studies were financially supported by German Primate Center, Volkswagen Foundation, various American and European zoos, and private persons. Due to this work, the current status of the species and conservation needs are well known, and the Lion-tailed Macaque is one of the best-studied macaque species, both in the wild and in captivity (for an overview see Singh et al. 2009 and Kaumanns et al. 2013). In situ and ex situ studies resulted in a large number of publications that cover aspects of husbandry and management, conservation and especially many aspects of the species biology. A number of Prof. Singh's students were involved in Lion-tailed Macaque studies and will continue working for the conservation of the species. Efforts to save the LTM in India got much support through the Fifth International LTM Conference in 1999, that was organised by Mewa Singh at the University of Mysore and supported by the EEP coordinator. Two volumes (58, 59) of German Primate Center's Primate Report (Schwibbe et al. 2000, 2001) report on the results of the conference. These reports provide an overview on the status of in situ and ex situ research and captive propagation efforts for the species.

The contact with Indian colleagues, the involvement in field studies on a number of aspects of the species biology, and the resulting knowledge, significantly influenced the management of the EEP population. From the beginning of the EEP's existence, the importance of behavioural and especially social aspects, breeding patterns and aspects of life histories were emphasised. According to Singh et al. (2006), especially considering the reproductive system and social system of the species, is the key to the conservation of the species. EEP policy strongly went for this. Although close cooperation between EEP and SSP was initiated during the Third International LTM Conference (1990) in San Diego, the programmes developed differently. In the SSP population, birth control on a large scale, based on a strict genetic management was carried out from about 1988 onwards (Lindburg & Gledhill 1992; Lindburg et al. 1997; Lindburg 2001). Figure 1 demonstrates the effects on the development of the global historical population. It also shows the latter's "recovery" (2001–2011) and a new decline from 2012 onwards. This results from a strong decrease in the number of births (Figure 2). This decrease is induced by the development of the European population (Figure 3). Birth control has been carried out there, too, to deal with space problems. Under these pressurising conditions, the EEP long-term management plan edited in 2016 (Sliwa et al. 2016) recommends further birth control measures on a large scale.

Birth control on a large scale over long periods of time to control population size, however, can have enormous risks for the survival of a population. The example of the SSP population and a number of relevant studies (Kaumanns et al. 2013; Penfold et al. 2014; Kaumanns & Singh 2015; Kaumanns et al. 2020) demonstrate possible negative consequences and elaborate ways to stop negative trends.

We are afraid that under the conditions given, the EEP population's and therefore the global captive population's, long-term survival is threatened – given the trend in population development continues and no serious changes in management are initiated soon. The 'Endangered' status of the LTM in the wild (Singh et al. 2020) with increasing fragmentation of its range of distribution and habitat destruction, strongly recommend, to continue with preserving a reserve in zoos, especially in India. Measures to stabilise the European and thus the global captive population, and new steps towards achieving its long-term survival are urgently required in order to prevent a loss of reproductive potential, like it happened in the SSP population. The European population is the only captive population that is still large and potentially productive enough to be developed further as a reserve. It seems, that space problems and other infrastructural limitations currently hinder to achieve this goal. EEP participants should consider whether all means to allow more breeding again are *really* exhausted or whether stopping birth control or more moderate schedules are possible, at least. It is suggested that more should be done to preserve the population's breeding potential, size, and structure, with the goal to send European LTMs back to other regions and especially to their country of origin.

Zoos in India keep a small LTM population with a number of potential founders. Many zoos however report breeding problems. According to the last edition of the international studbook, totally 51 animals are kept in 10 Indian zoos, six of which keep less than three animals each. There are two zoos with more individuals – Chennai (n= 20) and Trivandrum (n= 10). These group sizes come close to group sizes in the wild. Historically, Chennai Zoo contributed to more than one-third (n= 64) of the captive births in India (n= 185) and between 2003 and 2018, it contributed to 75% (n= 45) of births in Indian zoos (n= 60) in this period. This might be due to an accumulation of husbandry know-how, personnel experience, and constancy in the management system. Delhi Zoo played an important role in the past by contributing to 49 births, many of them in the 1970s–80s. Judging from the experiences in the European breeding programme, successful breeding requires allowing groups to grow undisturbed, to larger sizes of around 20 individuals with differentiated demographic structures that allow the females to live permanently in their natal groups and to maintain strong social bonds (female-bonded system; see Kumar 1987). This would allow intergenerational overlap and to acquire the necessary social and cognitive competence to interact properly in a complex social system and to raise offspring (Kaumanns et al. 2013). According to field observations, only the males are the mobile elements of the Lion-tailed Macaque social system (Kumar 1987; Kumar et al. 2001). Under captive conditions only males should be transferred between groups (for details see Kaumanns et al. 2006). More information derived from the studies in the wild (e.g., Kumar 1987; Krishnamani & Kumar 2000; Umapathy & Kumar 2000; Sharma 2002; Sushma 2004; Singh et al. 2006) is available to be used in designing keeping systems for the species. It refers to the species' arboreal life, selective and individualised foraging on diverse plant and animal species, seasonal variations in diet, large time spent in foraging and exploration, maintenance of large interindividual distances, low reproductive turnover, and a number of special features of the reproductive system. Many aspects have been emphasised for the management of the species in the international breeding programmes. Their consideration would also support successful breeding in the country of origin especially with its advantage of natural living conditions, availability of native food plants and large open-air enclosures.

The Indian zoo community is interested in building up a larger, more productive population in cooperation with the European Breeding Programme (Govindhaswamy Umapathy, pers. comm. 03.viii.2020). This constellation provides a chance to develop perspectives and solutions for problems on both sides. A cooperation could provide spaces for Lion-tailed Macaques from European zoos. Even more importantly, a larger and productive Indian population supported both in terms of animals and know-how from Europe could serve as an interface between the captive and the wild populations. It could be used for a number of conservation purposes – including providing animals for reintroductions in the long run. The establishment of an “Indo-European Lion-tailed Macaque reserve population” would require careful planning. An integrated (One-Plan) approach needs to be developed that aims at the integration of the know-how on the species and the conservation-oriented research interests as provided by the above-mentioned Indian scientists and their institutions. It furthermore should aim at the development of the infrastructural conditions in selected Indian zoos as required for an appropriate management and husbandry aiming at conservation breeding (for a more elaborated outline on this topic see Singh et al. 2012). Research institutions, selected Indian zoos in the range states of the species (like Chennai, Trivandrum, and Mysore) and the EEP should cooperate closely. A small board of experts from these institutions should be established to guide and supervise the project. Previous attempts to establish a breeding programme for the LTM in India and to transfer breeding groups from the USA and from Europe did not work out well due to bureaucratic issues and difficulties with local competence and motivation (see also Krishnakumar & Manimozhi 2000; Singh et al. 2009). The proposed new approach should be designed such that corresponding problems are minimised. It is of particular importance to ‘institutionalise’ captive propagation of the LTM in its country of origin more strongly. It should include to choose a competent coordinator who permanently overlooks and organises the work above the level of individual zoos and is supported by the Central Zoo Authority of India. A successfully carried out project would also serve as a model for other species and co-operations. It could help to establish Indian zoos as important partners in metapopulation management programmes especially concerning endemic Indian species like the LTM. It is important to note thereby, that time is running out for the development and establishment of international metapopulation management programmes (see Macdonald & Hofer 2011; Powell et al. 2019). They are needed to overcome the sustainability problems threatening many captive populations. Many of them are shrinking for instance due to breeding problems. In terms of climate, available space, and other resources, a number of zoos in India could establish very good keeping systems for the LTM. As elaborated by Singh et al. (2012), conservation breeding in Indian zoos, however, still requires a serious change in professional attitudes, training opportunities and infrastructural requirements. The future of the global captive population of the LTM, for instance, may depend on progress there.

Many zoos and many dedicated people in several countries worked for the survival of the LTM in the wild and for the establishment of a reserve population under human care over many decades. They achieved a lot. Currently, much of what has been achieved with the captive population is at risk. To allow a development ending with a captive LTM population without much breeding and thus with a low conservation potential would be against professional standards and simply sad.

References

Gledhill, L.G. (1985). Analysis of statistics submitted to the Lion-tailed Macaque studbook - North American zoos, pp. 237–238. In: Heltne, P.G. (ed.). *The Lion-tailed Macaque: Status and Conservation.* Alan R. Liss, New York, 411 pp.

Hill, C.A. (1971). Zoo’s help for a rare monkey. *Oryx* 11(1): 35–38. https://doi.org/10.1017/S003060530000942X

Kaumanns, W., E. Krebs & M. Singh (2006). An endangered species in captivity: Husbandry and management of the Lion-tailed Macaque *(Macaca silenus). MyScience* 1: 43–71.

Kaumanns, W., M. Singh & A. Sliwa (2013). Captive propagation of threatened primates–the example of the Lion-tailed Macaque *Macaca silenus*. *Journal of Threatened Taxa* 5(14): 4825–4839. https://doi.org/10.11609/JoTT.o3625.4825-39

Kaumanns, W. & M. Singh (2015). Towards more individual-based and fitness- oriented captive mammal population management. *Current Science* 109(6): 1121–1129. https://doi.org/10.18520/v109/i6/1121-1129

Kaumanns, W., N. Begum & H. Hofer (2020). “Animals are designed for breeding”: Captive population management needs a new perspective. *Journal of Zoo and Aquarium Research* 8(2): 76–85. https://doi.org/10.19227/jzar.v8i2.477

Krishnakumar, N. & A. Manimozhi (2000). What ails captive breeding programmes in India -Lion-tailed Macaque (LTM) - A case study. *Zoos’ Print* 15(5): 3–4.

Krishnamani, R. & A. Kumar (2000). Phyto-ecology of the Lion-tailed Macaque *(Macaca silenus)* habitats in Karnataka, India: Floristic structure and density of food trees. *Primate Report* 58: 27–56.

Kumar, A. (1987). The ecology and population dynamics of the Lion-tailed Macaque (*Macaca silenus*) in South India. PhD Thesis. University of Cambridge, 174pp.

Kumar, M.A., M. Singh, H.N. Kumara, A.K. Sharma & C. Bertsch (2001). Male migration in Lion-tailed Macaques. *Primate Report* 59: 5–18.

Lindburg, D.G., A.M. Lyles & N.M. Czekala (1989). Status and reproductive potential of Lion-tailed Macaques in captivity. *Zoo Biology Supplement* 1: 5–16.

Lindburg, D.G. & L.G. Gledhill (1992). Captive breeding and conservation of Lion- tailed Macaques. *Endangered Species Update* 10: 1–4.

Lindburg, D.G. & N.C. Harvey (1996). Reproductive biology of captive Lion-tailed Macaques, pp. 318–341. In: Fa, J.E. & D.G. Lindburg (eds.). *Evolution and Ecology of Macaque Societies.* Cambridge University Press, Cambridge, 597pp.

Lindburg, D.G., J. Iaderosa & L. Gledhill (1997). Steady-state propagation of captive Lion-tailed Macaques in North American zoos: A conservation strategy, pp. 131–150. In: Walli, J (ed.). *Primate Conservation: The Role of Zoological Parks*. American Society of Primatologists, Vol.1., Chicago, 252 pp.

Lindburg, D.G. (2001). A century of involvement with Lion-tailed Macaques in North America. *Primate Report* 59: 51–64.

Macdonald, A.A. & H. Hofer (2011). Editorial: Research in zoos. *International Zoo Yearbook* 45: 1–6. https://doi.org/10.1111/j.1748-1090.2011.00145.x

Ness, T. (2011). *North American Studbook for Lion-tailed Macaques* (*Macaca silenus*). Minnesota Zoological Gardens, Minnesota, 131 pp.

Ness, T. (2013). *North American Studbook for Lion-tailed Macaques* (*Macaca silenus*). Minnesota Zoological Gardens, Minnesota, 136 pp.

Penfold, L.M., D. Powell, K. Traylor-Holzer & C.S. Asa (2014). ‘Use it or lose it’: characterization, implications, and mitigation of female infertility in captive wildlife. *Zoo Biology* 33(1): 20–28. https://doi.org/10.1002/zoo.21104

Powell, D.M., C.L. Dorsey & L.J. Faust (2019). Advancing the science behind animal program sustainability: An overview of the special issue. *Zoo Biology* 38(1): 5–11. https://doi.org/10.1002/zoo.21474

Sarno, A. (2018). *North American Studbook for Lion-tailed Macaques* (*Macaca silenus*). Kansas City Zoo, Kansas City, 175 pp.

Schwibbe, M., M. Singh, W. Kaumanns & C. Knogge (Eds.) (2000). *Proceedings of the Fifth International Symposium on Lion-tailed Macaque, Mysore, India, Part 1. Primate Report 58.* German Primate Center, Goettingen, 95pp.

Schwibbe, M., M. Singh, W. Kaumanns & C. Knogge (Eds.) (2001). *Proceedings of the Fifth International Symposium on Lion-tailed Macaque, Mysore, India, Part 2. Primate Report 59.* German Primate Center, Goettingen, 108 pp.

Sharma, A.K. (2002). A study of reproductive behaviour of Lion-tailed Macaque *(Macaca silenus)* in the rainforests of Western Ghats. PhD Thesis. Department of Zoology, University of Mysore, 102 pp.

Singh, M., A.K. Sharma, E. Krebs & W. Kaumanns (2006). Reproductive biology of Lion-tailed Macaque (*Macaca silenus*): An important key to the conservation of an endangered species. *Current Science* 90(6): 804–811.

Singh, M., W. Kaumanns, M. Singh, H.S. Sushma & S. Molur (2009). The Lion- tailed Macaque *Macaca silenus* (Primates: Cercopihecidae): conservation history and status of a flagship species of the tropical rainforests of the Western Ghats, India. *Journal of Threatened Taxa* 1(3): 151–157. https://doi.org/10.11609/JoTT.o2000.151-7

Singh, M., W. Kaumanns & G. Umapathy (2012). Conservation-oriented captive breeding of primates in India: Is there a perspective? *Current Science* 103(12): 1399–1400. https://www.jstor.org/stable/24089343

Singh, M., A. Kumar & H.N. Kumara (2020). *Macaca silenus*. The IUCN Red List of Threatened Species 2020: e.T12559A17951402. Downloaded on 21 August 2021. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T12559A17951402.en

Sliwa, A., K. Schad & E. Fienieg (2016). Long-term management plan for the Lion- tailed Macaque (*Macaca silenus*) European Endangered Species Programme (EEP). Zoologischer Garten Köln, Köln, Germany and European Association of Zoos and Aquaria (EAZA), Amsterdam, Netherlands, 60 pp.

Sliwa, A. & N. Begum (2019). *International Studbook 2018 for the Lion-tailed Macaque Macaca silenus Linnaeus*, *1758, edition 2018, Vol. 9.* Zoologischer Garten Köln, Cologne, v+188 pp.

Sushma, H.S. (2004). Resource utilization and niche separation in sympatric rainforest arboreal mammals. PhD Thesis. University of Mysore, 150 pp.

Umapathy, G. & A. Kumar (2000). Impacts of the habitat fragmentation on time budget and feeding ecology of Lion-tailed Macaques (*Macaca silenus*) in rainforest fragments of Anamalai Hills, South India. *Primate Report* 58: 67–82.

Chapter 5: Publication 4

“Animals are Designed for Breeding”: Captive Population Management Needs a New Perspective

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Contributions of the authors

Werner Kaumanns and Nilofer Begum developed the concept and wrote the paper. Heribert Hofer commented and improved the paper by contributing important theoretical considerations.

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"Animals are designed for breeding": captive population management needs a new perspective

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Abstract

A key purpose of the management of captive populations of birds and mammals is their long-term viability (sustainability). This paper considers why many captive populations of birds and mammals face serious challenges and links their lack of sustainability directly to the management and diagnosis of breeding problems. Two well-known population management paradigms are the "small population paradigm" and the "declining population paradigm". The paper argues that under the latter, better management options can be developed, as they emphasise an analysis of the reasons for the decline and the role of the individual's breeding performance, compared to traditional captive management which follows recommendations derived from the small population paradigm. This paper suggests that it will be helpful to manage a population predominantly as a "breeding device" and to view its individual members as its constituents that are "designed for breeding". Following life history theory, individuals are best regarded as phenotypes that combine traits which contribute to individual variation in survival and reproductive success (fitness). Regarding individuals as the units of management with all their fitness-related properties allows the establishment of an integrated management approach that considers their various properties (genotype, ethotype, demotype, etc.) at the same level of importance. Management should then focus on key traits—those traits that are primary determinants of fitness in terms of breeding conditions in a given environment. With reference to the altered conditions of captivity, the paper emphasises the preservation of the breeding potential of a population. This means, in practice, to enable patterns of reproduction and corresponding life histories of natural populations in captivity as much possible, with the implication that this can generate larger population sizes, in turn creating a surplus of individuals needing to be dealt with appropriately. Genetic management, including the use of molecular DNA information, should be part of such an integrated management approach, be compatible with "natural" population dynamics and concentrate on breeding units.

Introduction

Ensuring the long-term survival of captive populations is currently one of the main problems of zoo biology. Sustainability problems are reported from a large number of breeding programmes (Kaumanns et al. 2000; Earnhardt et al. 2001; Barlow and Hibbard 2005; Baker 2007; Kaumanns et al. 2008; Lees and Wilcken 2009; Leus et al. 2011; Long et al. 2011; Che-Castaldo et al. 2019; McCann and Powell 2019). A recently published special issue of Zoo Biology provides an overview of the sustainability problems encountered in current American breeding programmes, presents approaches and analytical tools to deal with them, and conducts assessments of potential reasons for the problems (Powell et al. 2019). None of the contributions, however, discusses the basic validity of the management paradigm used so far, that evidently has contributed to or did not prevent the poor current status of many populations. It is suspected that, besides specific reasons for sustainability problems in specific populations, the management paradigm and policies used in many cases might have reduced the individuals' and populations' breeding potential (see Penfold et al. 2014). The various approaches and tools presented in the special issue will help to reduce sustainability problems in some populations. Here, it is proposed, however, that a change in management paradigm, and in particular the goal of management, would provide more opportunity for improvements and would likely prevent further maladaptive developments. It is proposed that declining captive populations should be managed according to the insights generated by the "declining population paradigm", to consider them as "breeding devices" and the individuals (in their breeding units) mainly as "units of reproduction". A necessary condition for a "healthy" captive population is successful breeding over long periods of time and the potential to transfer adaptive phenotypes into future generations. The presented approach is based on Caughley's (1994) influential paper on the conservation of free-ranging wildlife populations, in which he analyses basic scientific approaches in conservation biology, in particular with reference to the conservation of threatened populations, following on from earlier papers on the topic by Kaumanns (1994) and Kaumanns and Singh (2015). This paper will elaborate the conceptual background for, and the principles of, a corresponding management paradigm. The practical implementation of this general approach will vary between species and breeding programmes; therefore, the suggestions made in this paper remain on a general level.

Population management paradigms

According to Caughley (1994), concepts and practices used to support declining, threatened populations can differ depending on management paradigms and the ultimate goals chosen. Approaches that follow a "small population paradigm" aim to preserve "genetic raw material" for potential adaptation to future environmental changes and genetic diversity (see Frankel 1970, 1974; Frankel and Soulé 1981; Soulé et al. 1986; Lacy 1994; Frankham 2005). According to Caughley (1994), approaches following a "declining population paradigm" are not necessarily driven by genetics: preservation of "genetic raw material" might be integrated into a broader context of achieving survival of a population and maintaining or improving its adaptiveness. Other measures, aside from genetic management, might be regarded as more critical to the survival of a declining population (see Leader-Williams et al. 1990; Caro and Laurenson 1994; Courchamp et al. 1999; Asquith 2001). Recent extinctions can rarely, if ever, be attributed to a single cause and conservation actions, therefore, need to target multiple drivers (Brook 2008; Brook et al. 2008).

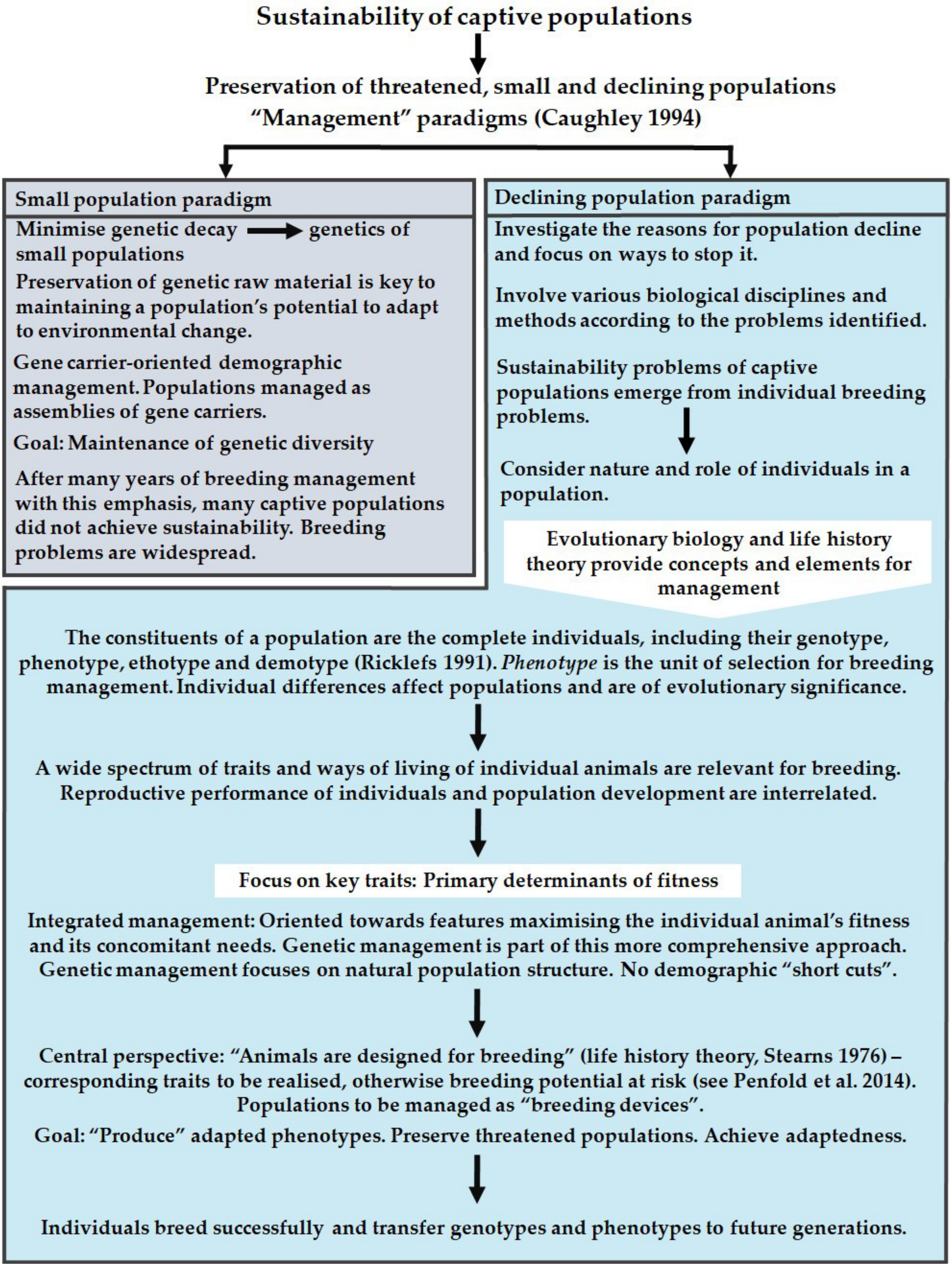
Many populations of wild animals in zoos are currently small and in a demographically poor state (Lees and Wilcken 2009; Leus et al. 2011; Che-Castaldo et al. 2019). Since the establishment of breeding programmes in the 1980s, population management has followed the "small population paradigm". Breeding programmes organised by the American and European zoo associations put much emphasis on managing genotypes in their populations (Ballou et al. 2010). This is mainly intended to minimise the rate of genetic decay (Lacy 1994, 2009). Individuals in a population are, therefore, predominantly managed as "gene carriers" (see Ballou et al. 2010). In practice, this often means that the overall altered nature of the captive population is not considered and that priority is not given to the potential loss of features essential for survival and adaptation (see Kaumanns et al. 2008, Kaumanns and Singh 2015). In particular, appropriate attention is not given to breeding problems and the insufficient development or decline of many captive populations over time (Lees and Wilcken 2009; Leus et al. 2011).

This paper suggests that stopping this decline requires a management approach with a broader perspective and more motivation to investigate the causes of decline. The "declining population paradigm" provides a framework for this, as it investigates the decline in viability of a (captive) population. To do so, it is necessary to consider reproductive biology within a captive setting, the reproductive system and breeding problems. Penfold et al. (2014) review studies on this topic. Low reproduction currently seems to be the most common challenge to population viability (Che-Castaldo et al. 2019), likely due to species-specific requirements. Conservation measures should, therefore, pay attention to species-specific breeding patterns and their resulting potential to reproduce and survive. Examples of this follow.

Fazio et al. (2018) found that breeding success in captive fishing cats (*Prionailurus viverrinus*) was low (only 2 out of 13 pairs produced offspring); where breeding was successful, it was positively associated with the availability of larger indoor areas and positive reinforcement training. Daigle et al. (2015) found that captive female African lions (*Panthera leo*) had a far lower reproductive span than wild counterparts (on average, captive females bred for only two years, between 4–6 years of age, compared to 12–13 years in the wild). This may be related to husbandry and loss of breeding-management knowledge. It is likely that individuals in declining captive populations are unable to access appropriate breeding conditions. The negative consequences of delaying breeding on the reproductive success of captive mammals has been demonstrated for African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) (Hildebrandt et al. 2000a; Hermes et al. 2004); white rhinoceros (*Ceratotherium simum*) (Hermes et al. 2006); and cheetah (*Acinonyx jubatus*) (Wachter et al. 2011; Ludwig et al. 2019). Evidently, it is of critical importance to investigate the influence of captive living conditions on breeding success (Wielebnowski et al. 2002; Brown et al. 2004; Walker et al. 2004; Saunders et al. 2014). There might be mismatches between species-typical adaptations, living conditions and management programmes. Princée and Glatston (2016), for instance, demonstrated that breeding problems in captive red pandas (*Ailurus fulgens*) resulted from females not finding appropriate rearing conditions for their offspring in many zoos located outside their natural climate zone; zoo conditions were too warm and humid.

The importance of the individual in population management

We suspect that mismatches in breeding conditions and breeding partners arising from a gene-carrier biased management approach regularly lead to breeding problems. In order to prevent this, Kaumanns and Singh (2015) proposed putting more emphasis on individuals as units of reproduction and considering their individual life histories and roles within a population. The authors suggested that life-history theory provides the relevant concepts, as it investigates the adaptive value of the individual's life history in a population. This concerns fitness-relevant sequences of major events and processes in the individual's lifetime, as well as the processes generating their temporal distribution, such as timing and intensity of reproduction (see Roff 1992; Stearns 1992; Daan and Tinbergen 1997). Evidently, much of what "happens" in a population and influences reproductive success is also (fitness) relevant, such as the introduction of novel predators or diseases in wild populations, or the death or removal of good breeders in a captive setting. Basically, "life history theory tries to explain how evolution designs organisms to achieve reproductive success" (Stearns 2000, p. 476). Life-history theory, therefore, justifies why fitness-relevant traits should guide population management. The starting point, and a key component of life-history theory, is that the individual phenotypes are the constituents of a population and are therefore under selection (see Ricklefs 1991; Stearns 2000; Hendry et al. 2011). As a consequence, the various levels (genotype, phenotype, ethotype, i.e. behaviour and physiological processes, and demotype, i.e. age-specific fecundity and survival value) of an individual are considered equally important for fitness maximisation and thus for management. Neglecting the importance of such a holistic approach will cause breeding problems in many captive settings and populations. For example, the behavioural skills of a primate female can be considered in



Sustainability of captive populations

Preservation of threatened, small and declining populations
"Management" paradigms (Caughley 1994)

Small population paradigm

Minimise genetic decay → genetics of small populations

Preservation of genetic raw material is key to maintaining a population's potential to adapt to environmental change.

Gene carrier-oriented demographic management. Populations managed as assemblies of gene carriers.

Goal: Maintenance of genetic diversity

After many years of breeding management with this emphasis, many captive populations did not achieve sustainability. Breeding problems are widespread.

Declining population paradigm

Investigate the reasons for population decline and focus on ways to stop it.

Involve various biological disciplines and methods according to the problems identified.

Sustainability problems of captive populations emerge from individual breeding problems.

Consider nature and role of individuals in a population.

Evolutionary biology and life history theory provide concepts and elements for management

The constituents of a population are the complete individuals, including their genotype, phenotype, ethotype and demotype (Ricklefs 1991). *Phenotype* is the unit of selection for breeding management. Individual differences affect populations and are of evolutionary significance.

A wide spectrum of traits and ways of living of individual animals are relevant for breeding. Reproductive performance of individuals and population development are interrelated.

Focus on key traits: Primary determinants of fitness

Integrated management: Oriented towards features maximising the individual animal's fitness and its concomitant needs. Genetic management is part of this more comprehensive approach. Genetic management focuses on natural population structure. No demographic "short cuts".

Central perspective: "Animals are designed for breeding" (life history theory, Stearns 1976) – corresponding traits to be realised, otherwise breeding potential at risk (see Penfold et al. 2014). Populations to be managed as "breeding devices".

Goal: "Produce" adapted phenotypes. Preserve threatened populations. Achieve adaptedness.

Individuals breed successfully and transfer genotypes and phenotypes to future generations.

Figure 1. Flow chart of approach.

the context of infant rearing. Her experience and aptitude in this respect are as relevant as her genetic status to reproductive success and recruitment for population management. It is, therefore, necessary that appropriate conditions are provided to ensure that females can acquire these skills. This can require the presence of aunts, mothers or other group members, an appropriate demography and group composition. Furthermore, this will not be restricted to primates: providing the setting for mothers to gain the necessary experience would also be beneficial in elephants and other species with complex societies, such as spotted hyenas (*Crocuta crocuta*, Hofer and East 2003).

Individuals within a population differ, and the differences among them affect the behaviour of the entire population (Łomnicki 1978, 1988, 1999). Lott (1984) discusses the evolutionary significance of intraspecific variation in behaviour and social systems of vertebrates. Phenotypic variation usually improves population persistence (Hendry et al. 2011). It is a key focus of evolutionary theory and of phenotype management approaches (see Watters and Meehan 2007; Kaumanns and Singh 2015; Watters et al. 2017). The "production" and preservation of different phenotypes requires a phenotype-oriented "habitat management" approach, as presented in Watters et al. (2003) for wild Pacific salmon (*Oncorhynchus spp.*) and desert pupfish (*Cyprinodon spp*.). Whether differences in captive living conditions would trigger the development of different phenotypes and personalities (e.g., "bold" versus "shy") and their adaptive value, is currently investigated and discussed (see Bremner-Harrison et al. 2004; Sinn et al. 2014; Dunston et al. 2016). Watters et al. (2017) provide a framework that considers the role of individual phenotypes for conservation and elaborates the applications of phenotype management for captive propagation, education and for release.

The concepts outlined above require population management to refer to a spectrum of (species-typical) traits and aspects of individuals to optimise conditions for breeding and sustainability. Furthermore, the life histories of individuals in natural conditions, including their behavioural decisions, are fitness relevant (see Ricklefs 1991; Daan and Tinbergen 1997; Stearns 2000; Stillman et al. 2015); therefore, corresponding events and patterns in captive populations should also be relevant to management. Griffith et al. (2017), for instance, reviewed and identified several environmental, husbandry, life-history and behavioural factors that potentially contribute to the extensive variation in the reproductive success of captive zebra finches (*Taeniopygia guttata*) and their overall low reproductive output.

Consequently, management plans and husbandry guidelines should consider the biology of a species. In order to identify the potential fitness-relevant traits within the simplified conditions of captivity, population management has to carefully work out which aspects of living conditions and traits require special attention. In this context, the concept of "key traits", proposed by Carroll and Watters (2008), may help organise the complexities in practice. A "key trait" is a primary determinant of fitness for a given condition. Key traits may belong to different functional areas: they might refer to a species' feeding ecology, predator avoidance including vigilance behaviour, flight distance and the tendency to flee, social life, reproduction, and others. The key traits of a species should play a dominant role in developing husbandry guidelines and recommendations for breeding programmes. Below is a brief discussion of several examples.

A key trait relevant to the management of some great ape species is their fission-fusion social systems (see Classen et al. 2016). Husbandry perspectives often neglect to distinguish between primates that naturally occur in permanent groups and those that only come together under certain conditions.

A key trait relevant to the management of the lion-tailed macaque (*Macaca silenus*) in captivity is its female-bonded social system, common to most macaques (Lindburg 1991; Thierry et al. 2004). Lion-tailed macaque groups comprise 15–20 individuals, with genetically related females living together on a permanent basis and relationships often characterised by strong social bonds (see Kumar 1987). They are hierarchically organised in clans (Singh et al. 2006), in which males are the mobile elements, with dispersal occurring frequently (Kumar 1987). Females compete for access to males during oestrous (Kumar 2000), and prefer "new" males (Kumar et al. 2001). A challenge to captive husbandry is, therefore, to manage both dispersal and immigration events; for these and other management implications see Kaumanns et al. (2006, 2013).

In whooping cranes (*Grus americana*), Teitelbaum et al. (2017) described patterns of pair formation, including mate choice structures, that, according to Brown et al. (2019), might be of particular importance to successful breeding and, therefore, could be regarded as a key trait for the species. Several studies have shown that providing mate choice opportunities and familiarising potential partners with each other can improve reproductive success (cheetah: Mossotti 2010; Columbia Basin pygmy rabbits, *Brachylagus idahoensis*: Martin and Shepherdson 2012; giant panda, *Ailuropoda melanoleuca*: Martin-Wintle et al. 2015; eastern barred bandicoot, *Perameles gunnii*: Hartnett et al. 2018).

Many adaptive behavioural patterns, systems and mechanisms are conservative and inflexible and can constrain social interactions and the reproductive system under inappropriate living conditions (see Blumstein 2010; Kaumanns and Singh 2015). Other traits may provide more flexibility and plasticity to animals, especially in altered living conditions. The development of new foraging techniques and the use of novel foods are examples (Singh et al. 2001; Sih et al. 2011; Tuomainen and Candolin 2011). Recent studies investigating how animals cope with "human-induced rapid environmental change" ("HIREC") emphasise the role of behavioural systems and adaptations in this context (Sih et al. 2011; Sih 2013). Key traits may be central elements in the establishment of species-typical life-history patterns.

An integrated management approach is required

Day-to-day management and husbandry procedures deal with the individuals of a population and their living conditions, on one hand, and the "gene-carrier" based (long-term) population management as propagated in the "small population paradigm", on the other hand. These two approaches have so far not interacted in a productive way so as to result in the establishment of sustainable populations. Lacy (2013) elaborates on the limitations of current population management and suggests that an integrated management approach might help overcome sustainability problems; this approach needs further development. More precisely, well-established methods of kinship-based pedigree management should integrate the management of quantitative genetic variation, molecular variation and behavioural variation. However, this approach might not go far enough: the method may change but the target does not. The approach would still focus on the ("external") goal to establish specific future genetic properties of the population. These properties are regarded as a critical reference system for management and a condition for the conservation potential of the population. They are, thus, prioritised over fitness-relevant behaviours and other adaptive traits, especially with reference to the reproductive system. Lacy (2013) notes that, since we cannot trust that "all forms of adaptive variation will be maintained along with the modelled neutral genetic variation, we will need to monitor morphological, behavioural, and physiological variation".

Management that aims to achieve the persistence of a population "forcefully", via rigid demographic management at the genotype level, is at risk of overburdening the individual's coping potential. It may hinder the animal from developing an "integrated" fitness-seeking way of life. For instance, when lion-tailed macaques are kept in groups of no more than three non-related, adults (see Lindburg 1992) for reasons of genetic management (see Lindburg et al. 1997), they may not develop the required behaviours and mechanisms for problem-solving in their physical and social environments. For example, it is more difficult for unrelated, less familiar females to resolve conflicts, and it is more likely to result in biting wounds, than it is for related, familiar females (see Lindburg and Lasley 1985). Individuals in small groups are unlikely to develop rich and differentiated socialisation and learning repertoires (see Lindburg 1992). In effect, this is like subjecting individuals to extreme demographic conditions, which can profoundly affect social behaviour, social climate and individual fitness, as shown in primates (Altmann and Altmann 1979; Datta 1983a, 1983b).

To support integrated husbandry and population management, the approach must be fully oriented and integrated towards individual animals (fitness-maximising features and needs) and corresponding captive-living conditions. Genetic management and genetic diversity must be achieved by integrating corresponding management procedures into this framework. A management that considers the individual constituents of a population must also specifically consider the individual's basic design, as investigated by life-history theory.

"Animals are designed for breeding"

It is a central concept in evolutionary biology and life-history theory that animals, with their traits and adaptations, are ultimately designed for surviving and breeding (Stearns 1976, 2000). The focus on individuals as constituents of a population requires considering features resulting from their "basic design", often known as the "Bauplan". Next to survival, evolution places heavy emphasis on reproduction and the success of this profoundly affects the animal's contribution to future generations (Stearns 1976, 2000). Therefore, captive propagation and population management must consider this, particularly if the sustainability of the captive population is in doubt. Aside from breeding, population management of captive animals also involves limiting reproduction because of space limitations and other reasons (see e.g. Glatston 1998; Asa and Porton 2005). It seems evident that an animal "designed for breeding" requires (captive) living conditions that allow and support the realisation of these traits and adaptations on a large scale, if long-term population survival via breeding is attempted. Inappropriate management may trigger these traits to function as constraints. Penfold et al. (2014) investigated, in a retrospective analysis, the negative effects of prolonged periods of non-breeding on the fertility of females of multiple species housed in zoos. The authors demonstrate that, in captive populations, the reproductive system and productivity are fragile. The study also demonstrates the need for a better management of the reproductive system. The resulting recommendations by the authors, summarised under "use it or lose it", might be better substituted by "all-or-nothing" instead of limited use being enough. Considering life-history theory, adaptations related to the reproductive system (at the level of physiology and behaviour), might require the realisation of numerous traits and adaptations in many individuals of both sexes: most individuals have to breed in a species-typical pattern in order to maintain variation in life history, genetics, demography and behaviour. Effective population size should therefore be high. Otherwise, it is likely for maladaptive developments in the patterns of reproductive output and long-term population dynamics to arise (see Penfold et al. 2014), decreasing the breeding potential. Any intended or unintended reduction in a population's productivity (hindering individuals to breed via birth control or suboptimal living conditions) bears the risk of further impeding the population's development towards sustainability. This may be a consequence of directly or indirectly reducing the individual's reproductive potential (see Penfold et al. 2014), thus inducing vicious circles and supporting Allee effects (see below). The argument could be extended to state that species that have naturally low effective population sizes (because their social organisation and breeding regime involves only a small number of successful individuals), will be less suited to standard captive conditions.

Since even under optimal conditions, not all potential breeders in a population breed regularly, it is important to monitor and control effective population size continuously. Sambatti et al. (2008) elaborate the importance of effective population size for the conservation of fragmented populations. Although a number of studies demonstrate how, for instance, the behaviour of individuals can influence the effective population size (Parker and Waite 1997; Creel 1998; Blumstein 1998; Anthony and Blumstein 2000), the importance of such factors is often underestimated in breeding programmes.

Essentially, the approach outlined above suggests emphasising the link between individual breeding performance and population development (and long-term survival) in management concepts. Captive populations that are temporarily or partly restrained from reproducing are likely to lose their breeding potential. Overall, the long-term survival of a population depends on how well the individuals are managed, with special reference to their reproductive system and breeding performance. This includes preserving the individual's reproductive potential and achieving predictable individual patterns of reproduction as much as possible. The latter has to be based on an analysis of the population's (long-term) development, with special reference to the reproductive output of the individuals and of the breeding units in the historical population (see Princée 2016; Bauman et al. 2019). The demographic structures and (individual) patterns of reproduction in the history of a population should be considered when predicting their further development. An analysis of life-history patterns in the historical population should be carried out. The results should be compared with patterns in wild populations, if available. Possible discrepancies may point to critical aspects for management and possible reasons for breeding and other problems.

An ongoing analysis of the global captive population of the lion-tailed macaque, for instance, reveals low individual reproductive output, unfavourable demographic structures and resulting life-history patterns that deviate from those in the wild. Conditions required for the realisation of species-typical adaptations, such as living in permanent female-bonded social groups, have not been available to a large number of individuals over decades and generations, thus affecting fitness (Kaumanns et al. 2013; Begum in prep.). Primates and many other socially living animal species have to experience appropriate species-typical socialisation conditions to acquire social competence (Thornton and Clutton-Brock 2011; Lonsdorf and Ross 2012; Taborsky et al. 2012; Taborsky and Oliveira 2012; van Leeuwen et al. 2014; Alberts 2019). On a proximate level, these may be linked to species-typical life-history patterns, such as the number of infants per female in a group, group size, the degree of generational overlap and other parameters.

It is particularly important to consider how to preserve the breeding potential in a population. Since space limitations and/ or suboptimal demographic structures often do not allow optimal breeding conditions and population size, populations will evidently suffer. Problems may differ between species but may lead to the occurrence of Allee effects, which represent a reduction in fitness (Allee 1931; Courchamp et al. 2008). In addition, captive populations represent an extreme case of fragmentation, with negative consequences for productivity and sustainability (Singh and Kaumanns 2005; Kaumanns et al. 2008; Mason et al. 2013). When considering the discord between problems and conflicts resulting from limited space and related constraints, and the fastidious management necessary to achieve a sustainable population as outlined above, it is clearly necessary to be realistic about the potential of zoos to establish sustainable insurance populations Furthermore, additional research is required on the effects of altered living conditions on the long-term survival of populations. Zoos are sometimes regarded as models for wild populations confronted with altered living conditions (Mason et al. 2013). Zoo biologists have investigated particular problems resulting from, for instance, monotonous living conditions (see Watters 2009), or inappropriate feeding regimes (Schwitzer et al. 2002; Schwitzer and Kaumanns 2003). The consequences of keeping highly fragmented populations, such as the facilitation of Allee effects, are rarely investigated (but see Swaisgood and Schulte 2010). To achieve successful conservation-oriented captive propagation, a concentration on fewer animal species is recommended (Conway 2011; Lacy 2013; McCann and Powell 2019). Furthermore, the development of more flexible holding systems that incorporate the essentials of a species' niche or habitat is required. It should be propagated, for instance, to allow mate choice (e.g. Asa et al. 2011; Martin-Wintle et al. 2019), or for breeding males to be exchanged or "group encounters" to be arranged (e.g. Kaumanns et al. 1998; Zinner et al. 2001) in a routine manner.

How should genetic management be carried out?

Genetic management is an essential component of captive population management (see Soulé and Wilcox 1980). In particular, the use of molecular DNA information can play an important role in conservation breeding (Fienig and Galbusera 2013; Norman et al. 2019). Its integration into a more comprehensive management approach, as proposed above, requires orientation towards structures and processes that influence genetic structures in natural populations (see Keane et al. 1996; Sugg et al. 1996; Keller and Arcese 1998; Kokko and Ots 2006; Puurtinen 2011; Becker et al. 2012). Demographic structures and dynamics in free-ranging conditions are influenced by births and deaths, individual-based behavioural patterns and processes such as mate choice, dispersal of males or females, migration or pair formation under the given ecological conditions. Together they may provide an adaptive framework that influences a population's genetic status and diversity. A population's adaptiveness will therefore depend on the consistent availability of living conditions that fit with the individual's adaptations and requirements for successful reproduction.

When using the "short cut" of a rigid, "gene-carrier based" demographic management in captivity, requirements relating to the individual's traits and needs for successful breeding may not be met. According to Hendry et al. (2011 p. 161), "an understanding of phenotypes therefore should precede an understanding of genotypes". An integrated genetic management would have to avoid such short cuts by executing gene-carrier based demographic manipulations only in the context of the (adaptive) species-typical breeding units. It might, therefore, take longer to achieve the intended genetic composition; but it would also increase the chance of "producing" individuals that have the potential to breed and thus contribute to future generations. According to Ballou et al. (2010), genetic goals might have to be compromised under certain conditions (e.g. breeding problems in very small populations), by, for instance, inducing more breeding via genetically less-valuable individuals. "Compromising genetic goals" might occasionally happen in nature, resulting in surviving populations (see, e.g., Kokko and Ots 2006).

There is an additional and very interesting conflict of interests and goals to resolve. Much current thinking regarding genetic management (and the resulting breeding programmes) stipulates that reproduction should take place as late as possible in a captive individual's lifetime (Frankham 2008; Williams and Hoffman 2009). Thus, it is advised to increase generation time and dilute the possible selection pressures in the captive environment (Kraaijeveld-Smit et al. 2006) that may encourage reproduction. Otherwise, it is believed that animals would lose their ability to cope with natural conditions, should they become part of a re-introduction project. As shown by the examples of the cheetah (Wachter et al. 2011, Ludwig et al. 2019), rhinos, elephants and other species, this leads to the asymmetric reproductive aging of individuals; that is, the faster aging of the reproductive organs relative to the rest of the body (Hildebrandt et al. 2000a,b; Hermes et al. 2004). This is the strongest evidence to date that animals are designed for breeding: in particular, reasonably early breeding within their potential reproductive period (but see Frankham et al. 2002). In order to prevent irreversible asymmetric reproductive aging and a reduced reproductive lifespan, captive breeding should (1) start with breeding females as young adults (Hermes et al. 2004), and (2) encourage lactation until the natural age of weaning, as it prevents frequent fluctuation of oestrogen concentrations (Schmidt et al. 1983).

Successful breeding leads to space and "surplus" problems

Successful breeding on a large scale is a condition for the long-term survival of captive populations (see Penfold et al. 2014). It seems almost inevitable that this leads to space and "surplus" animals, not by accident, but as part of the intended strategic orientation of the management plan. If the establishment of conservation insurance populations is necessary and intended, this issue of surplus animals needs to be considered and solved. Under natural conditions, population size is regulated via birth rates and mortality, which are subject to both bottom-up and top-down ecological factors, such as food availability, predation or pathogens. One way to limit population size in captivity is to euthanise individuals, mimicking the effects of food shortage, predation or pathogens (see Lacy 1995). A more favoured option might be the design and organisation of conservation breeding and population management in such a way that zoological gardens and conservation efforts for free-ranging populations in range countries are an integral part of planning and management (see also "One-Plan approach", Byers et al. 2013; Gusset and Dick 2013, Traylor-Holzer et al. 2019). Currently, the political and logistic conditions for conservation in many range countries may not yet provide appropriate conditions for practical implementation (for India see Singh et al. 2012). The future of several captive populations may depend on rapid progress towards realising an integrated conservation management plan in range countries. For instance, in the case of the lion-tailed macaque, Singh et al. (2009, 2012) analyse the problems associated with its conservation in India and provide a perspective for conservation-oriented breeding of primates. Kaumanns et al. (2019) discuss in detail the possible consequences and perspectives for the future of the global captive population of lion-tailed macaque, also with reference to the role of Indian institutions.

References

Alberts S.C. (2019) Social influences on survival and reproduction: insights from a long-term study of wild baboons. *Journal of Animal Ecology* 88: 47–66. doi: 10.1111/1365-2656.12887

Allee W.C. (1931) *Animal Aggregations: A Study in General Sociology*. Chicago, Illinois: University of Chicago Press. doi: 10.5962/bhl.title.7313

Altmann S.A., Altmann J. (1979) Demographic constraints on behaviour and social organization. In Bernstein, I.S. and Smith, E.O. (eds). *Primate Ecology and Human Origins.* New York, NY: Garland STMP Press, 47–64.

Anthony L.L., Blumstein D.T. (2000) Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce Ne. *Biological Conservation* 95: 303–315. doi: 10.1016/S0006-3207(00)00037-9

Asa C.S., Porton I.J. (eds) (2008) *Wildlife Contraception – Issues, Methods, and Applications*. Baltimore, Maryland: John Hopkins University Press.

Asa C.S., Traylor-Holzer K., Lacy R.C. (2011) Can conservation-breeding programmes be improved by incorporating mate choice? *International Zoo Yearbook* 45: 203–212. doi: 10.1111/j.1748-1090.2010.00123.x

Asquith N.M. (2001) Misdirections in conservation biology. *Conservation Biology* 15: 345–352.

Baker A. (2007) Animal ambassadors: an analysis of the effectiveness and conservation impact of ex situ breeding efforts. In: Zimmermann, A., Hatchwell, M., Dickie, L. and West, C. (eds). *Zoos in the 21st Century: Catalyst for Conservation?* Cambridge, UK: Cambridge University Press, 139–154.

Ballou J.D., Lees C., Faust L.J., Long S., Lynch C., Lackey L.B., Foose T.J. (2010) Demographic and genetic management of captive populations. In: Kleiman, D.G., Thompson, K. and Kirk Baer, C. (eds). *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* 2nd Edition. Chicago, Illinois: The University of Chicago Press, 219–252.

Barlow S.C., Hibbard C. (2005) 'Going, going, gone. A zoo without exotic mammals?' *ARAZPA Submission* 148b: 1–12.

Bauman K., Sahrmann J., Franklin A., Asa C., Agnew M., Traylor-Holzer K., Powell D. (2019) Reproductive Viability Analysis (RVA) as a new tool for ex situ population management. *Zoo Biology* 38: 55–66. doi: 10.1002/zoo.21477

Becker P.A., Miller P.S., Gunther M.S., Somers M.J., Wildt D.E., Maldonado J.E. (2012) Inbreeding avoidance influences the viability of reintroduced populations of African wild dogs (*Lycaon pictus*) *PLoS ONE* 7: e37181. doi: 10.1371/journal.pone.0037181

Blumstein D.T. (1998) Female preferences and effective population size. *Animal Conservation* 1: 173–177. doi: 10.1111/j.1469-1795.1998.tb00026.x

Blumstein D.T. (2010) Social behaviour in conservation. In: Székely, T., Moore, A.J. and Komdeur, J. (eds). *Social behaviour: Genes, Ecology and Evolution.* Cambridge, UK: Cambridge University Press, 654–672.

Bremner-Harrison S., Prodohl P.A., Elwood R.W. (2004) Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation* 7: 313–320. doi: 10.1017/s1367943004001490

Brook, B.W. (2008) Demographics versus genetics in conservation biology. In: Carroll, S.P. and Fox, C.W. (eds). *Conservation Biology: Evolution in Action*. New York, NY: Oxford University Press, 35–49.

Brook B.W., Sodhi N.S., Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23: 453–460. doi: 10.1016/j.tree.2008.03.011

Brown J.L., Olson D., Keele M., Freeman E.W. (2004) Survey of the reproductive cyclicity status of Asian and African elephants in North America. *Zoo Biology* 23: 309–321. doi: 10.1002/zoo.20006

Brown M.E., Keefer C.L., Songsasen N. (2019) Factors affecting captive whooping crane egg fertility: a retrospective analysis. *The Journal of Wildlife Management* 83: 1377–1386. doi: 10.1002/jwmg.278787871717

Byers O., Lees C., Wilcken J., Schwitzer C. (2013) The one plan approach: the philosophy and implementation of CBSG's approach to integrated species conservation planning. *WAZA Magazine* 14: 2–5.

Caro T.M., Laurenson M.K. (1994) Ecological and genetic factors in conservation: a cautionary tale. *Science* 263: 485–486. doi: 10.1126/science.8290956

Carroll S.P., Watters J.V. (2008) Managing phenotypic variability with genetic and environmental heterogeneity: Adaptation as a first principle of conservation practice. In: Carroll, S.P. and Fox, C.W. (eds). *Conservation Biology: Evolution in Action*. New York, NY: Oxford University Press, 183–200.

Caughley G. (1994) Directions in conservation biology. *The Journal of Animal Ecology* 63: 215–244. doi: 10.2307/5542

Che-Castaldo J., Johnson B., Magrisso N., Mechak L., Melton K., Mucha K., Terwilliger L., Theis M., Long S., Faust L. (2019) Patterns in the long-term viability of North American zoo populations. *Zoo Biology* 38: 78–94. doi: 10.1002/zoo.21471

Classen D., Kiessling S., Mangalam M., Kaumanns W., Singh M. (2016) Fission–fusion species under restricted living conditions: a comparative study of dyadic interactions and physical proximity in captive bonobos and Bornean orangutans. *Current Science* 110: 839–850. doi: 10.18520/cs/v110/i5/839-850

Conway W.G. (2011) Buying time for wild animals with zoos. *Zoo Biology* 30: 1–8. doi: 10.1002/zoo.20352

Courchamp F., Berec L., Gascoigne J. (2008) *Allee Effects in Ecology and Conservation*. Oxford, Oxford University Press.

Courchamp F., Clutton-Brock T., Grenfell B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* 14: 405–410. doi: 10.1016/S0169-5347(99)01683-3

Creel S. (1998) Social organization and effective population size in carnivores. In: Caro, T. (ed). *Behavioral Ecology and Conservation Biology*. New York, NY: Oxford University Press, 246–265.

Daan S., Tinbergen J.M. (1997) Adaptations and life histories. In: Krebs, J.R. and Davies, N.B. (eds). *Behavioural Ecology: An Evolutionary Approach*. 4th Edition. Oxford, UK: Blackwell Science, 311–333.

Daigle C.L., Brown J.L., Carlstead K., Pukazhenthi B., Freeman E.W., Snider R.J. (2015) Multi-institutional survey of social, management, husbandry and environmental factors for the SSP African lion *Panthera leo* population: examining the effects of a breeding moratorium in relation to reproductive success. *International Zoo Yearbook* 49: 198–213. doi: /10.1111/izy.12073

Datta S.B. (1983a) Relative power and the maintenance of dominance. In: Hinde, R.A. (ed). *Primate Social Relationships – An Integrated Approach.* Oxford, UK: Blackwell, 103–112.

Datta S.B. (1983b) Relative power and the acquisition of rank. In: Hinde, R.A. (ed). *Primate Social Relationships – An Integrated Approach.* Oxford, UK: Blackwell, 93–103.

Dunston E.J., Abell J., Doyle R.E., Evershed M., Freire R. (2016) Exploring African lion (*Panthera leo*) behavioural phenotypes: individual differences and correlations between sociality, boldness and behaviour. *Journal of Ethology* 34: 277–290. doi: 10.1007/s10164-016-0473-9

Earnhardt J.M., Thompson S.D., Marhevsky E.A. (2001) Interactions of target population size, population parameters, and program management on viability of captive populations. *Zoo Biology* 20: 169–183. doi: 10.1002/zoo.1018

Fazio J.M., Freeman E.W., Bauer E., Rockwood L., Parsons E.C.M. (2019) Evaluation of management in North American zoos to enhance breeding success of the fishing cat (*Prionailurus viverrinus*) ex situ population. *Zoo Biology* 38: 189–199. doi: 10.1002/zoo.21465

Fienieg E.S., Galbusera P. (2013) The use and integration of molecular DNA information in conservation breeding programmes: a review. *Journal of Zoo and Aquarium Research* 1: 44–51.

Frankel O.H. (1970) Variation —The essence of life. *Proceedings of the Linnean Society of New South Wales* 95: 158–169.

Frankel O.H. (1974) Genetic conservation: our evolutionary responsibility. Genetics 78: 53–65.

Frankel O.H., Soulé M.E. (1981) *Conservation and Evolution*. Cambridge, UK: Cambridge University Press.

Frankham R. (2005) Genetics and extinction. *Biological Conservation* 126: 131–140. doi: 10.1016/j.biocon.2005.05.002

Frankham R. (2008) Genetic adaptation to captivity in species conservation programs. *Molecular Ecology* 17: 325–333. doi: 10.1111/j.1365-294X.2007.03399.x

Frankham R., Ballou J.D., Briscoe D.A. (2002) *Introduction to Conservation Genetics*. Cambridge, UK: Cambridge University Press.

Glatston R. (1998) The control of zoo populations with special reference to primates. *Animal Welfare* 7: 269–281.

Griffith S.C., Crino O.L., Andrew S.C., Nomano F.Y., Adkins-Regan E., Alonso-Alvarez C., Bailey I.E., Bittner S.S., Bolton P.E., Boner W., Boogert N., Boucaud I.C.A., Briga M., Buchanan K.L., Caspers B.A., Cichoń M., Clayton D.F., Derégnaucourt S., Forstmeier W., Guillette L.M., Hartley I.R., Healy S.D., Hill D.L., Holveck M.J., Hurley L.L., Ihle M., Krause E. T., Mainwaring M.C., Marasco V., Mariette M.M., Martin-Wintle M.S., McCowan L.S.C., McMahon M., Monaghan P., Nager R.G., Naguib M., Nord A., Potvin D.A., Prior N.H., Riebel K., Romero-Haro A.A., Royle N.J., Rutkowska J., Schuett W., Swaddle J.P., Tobler M., Trompf L., Varian-Ramos C.W., Vignal C., Villain A.S., Williams T.D. (2017) Variation in reproductive success across captive populations: methodological differences, potential biases and opportunities. *Ethology* 123: 1–29. doi: 10.1111/eth.12576

Gusset M., Dick G. (eds) (2013) Towards Integrated Species Conservation. *WAZA Magazine* 14. Gland, Switzerland: WAZA Executive Office.

Hartnett C.M., Parrott M.L., Mulder R.A., Coulson G., Magrath M.J.L. (2018) Opportunity for female mate choice improves reproductive outcomes in the conservation breeding program of the eastern barred bandicoot (*Perameles gunnii*). *Applied Animal Behaviour Science* 199: 67–74. doi: 10.1016/j.applanim.2017.10.008

Hendry A.P., Kinnison M.T., Heino M., Day T., Smith T.B., Fitt G., Bergstrom C.T., Oakeshott J., Jørgensen P.S., Zalucki M.P., Gilchrist G., Southerton S., Sih A., Strauss S., Denison R.F., Carroll S.P. (2011) Evolutionary principles and their practical application. *Evolutionary Applications* 4: 159–183. doi: 10.1111/j.1752-4571.2010.00165.x

Hermes R., Hildebrandt T.B., Göritz F. (2004) Reproductive problems directly attributable to long-term captivity-asymmetric reproductive aging. *Animal Reproduction Science* 82–83: 49–60. doi: 10.1016/j.anireprosci.2004.05.015

Hermes R., Hildebrandt T.B., Walzer C., Göritz F., Patton M.L., Silinski S., Anderson M.J., Reid C.E., Wibbelt G., Tomasova K., Schwarzenberger F. (2006) The effect of long non-reproductive periods on the genital health in captive female white rhinoceroses (*Ceratotherium simum simum, C. s. cottoni*). *Theriogenology* 65: 1492–1515. doi: 10.1016/j.theriogenology.2005.09.002

Hildebrandt T.B., Göritz F., Pratt N.C., Brown J.L., Montali R.J., Schmitt D.L., Fritsch G., Hermes R. (2000a) Ultrasonography of the urogenital tract in elephants (*Loxodonta africana* and *Elephas maximus*): an important tool for assessing female reproductive function. *Zoo Biology* 19: 321–332. doi: 10.1002/1098-2361(2000)19:5<321::AID-ZOO4>3.0.CO;2-K

Hildebrandt T.B., Hermes R., Pratt N.C., Fritsch G., Blottner S., Schmitt D.L., Ratanakorn P., Brown J.L., Rietschel W., Göritz F. (2000b) Ultrasonography of the urogenital tract in elephants (*Loxodonta africana* and *Elephas maximus*): an important tool for assessing male reproductive function. *Zoo Biology* 19: 333–345. doi: 10.1002/1098-2361(2000)19:5<333::AID-ZOO5>3.0.CO;2-A

Hofer H., East M.L. (2003) Behavioural processes and costs of co-existence in female spotted hyenas: a life history perspective. *Evolutionary Ecology* 17: 315–331. doi: 10.1023/A:1027352517231.

Kaumanns W. (1994) The quality of captive primate populations. *Primate Report* 39: 127–132.

Kaumanns W., Krebs E., Singh M. (2006) An endangered species in captivity: husbandry and management of the lion-tailed macaque (*Macaca silenus*). *MyScience* 1: 43–71.

Kaumanns W., Schwitzer C., Klumpe K., Schmid P. (2000) How are primate breeding programmes doing? An overview and preliminary analysis. In: Rietkerk, F., Hiddinga, B., Brouwer, K. and Smits, S. (eds). *EEP Yearbook* 1998/99. Amsterdam, Netherlands: EAZA Executive Office, 448–460.

Kaumanns W., Singh M. (2015) Towards more individual-based and fitness-oriented captive mammal population management. *Current Science* 109: 1121–1129. doi: 10.18520/v109/i6/1121-1129

Kaumanns W., Singh M., Begum N., Sliwa A. (2019) The captive population of the lion-tailed macaque *Macaca silenus*. In: Sliwa, A. and Begum, N. *International Studbook 2018 for the Lion-tailed Macaque Macaca silenus Linnaeus, 1758* Edition 2018 Vol. 9. Zoologischer Garten Köln, Germany, 5–11.

Kaumanns W., Singh M., Krebs E., Schwitzer C. (2008) Primate populations in zoos: a case of fragmentation. *Primate Report* 76: 41–54.

Kaumanns W., Singh M., Sliwa A. (2013) Captive propagation of threatened primates – the example of the lion-tailed macaque *Macaca silenus. Journal of Threatened Taxa* 5: 4825–4839.

Kaumanns W., Zinner D., Hindahl J. (1998) Experimentelle Gruppenbegegnungen als Mittel zur sozialen Stimulans bei in Menschenhand gehaltenen Bartaffen (*Macaca silenus*). *Zoologischer Garten* 68: 45–55.

Keane B., Creel S.R., Waser P.M. (1996) No evidence of inbreeding avoidance or inbreeding depression in a social carnivore. *Behavioral Ecology* 7: 480–489. doi: 10.1093/beheco/7.4.480

Keller L.F., Arcese P. (1998) No evidence for inbreeding avoidance in a natural population of song sparrows (*Melospiza melodia*). *American Naturalist* 152: 380–392. doi: 10.1086/286176

Kleiman D.G., Thompson K., Kirk Baer C. (eds) (2010) *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* 2nd Edition. Chicago, Illinois: The University of Chicago Press.

Kokko H., Ots I. (2006) When not to avoid inbreeding. *Evolution* 60: 467–475. doi: 10.1111/j.0014-3820.2006.tb01128.x

Kraaijeveld-Smit F.J.L., Griffiths R.A., Moore R.D., Beebee T.J.C. (2006) Captive breeding and the fitness of reintroduction species: a test of the response to predators in a threatened amphibian. *Journal of Applied Ecology* 43: 360–365. doi: 10.1111/j.1365-2664.2006.01137.x

Kumar A. (1987) The Ecology and Population Dynamics of the Lion-tailed Macaque (*Macaca silenus*) in South India. PhD thesis. Cambridge, UK: University of Cambridge.

Kumar A. (2000) Sexual harassment among female lion-tailed macaques (*Macaca silenus*) in the wild. *Journal of Bombay Natural History Society* 97: 42–51.

Kumar M.A., Singh M., Kumara H.N., Sharma A.K., Bertsch C. (2001). Male migration in lion-tailed macaques. *Primate Report* 59: 5–18.

Lacy R.C. (1994) Managing genetic diversity in captive animals. In: Bowles, M.L. and Whelan, C.J. (eds). *Restoration of Endangered Species.* Cambridge, UK: Cambridge University Press, 63–89.

Lacy R.C. (1995) Culling surplus animals for population management. In: Norton, B.G., Hutchins M., Stevens, E.F. and Maple T.L. (eds). *Ethics on the Ark: Zoos, Animal Welfare, and Wildlife Conservation.* Washington DC, USA: Smithsonian Institution Press, 187–194.

Lacy R.C. (2009) Stopping evolution: genetic management of captive populations. In: Amato, G., DeSalle, R., Ryder, O.A. and Rosenbaum, H.C. (eds). *Conservation Genetics in the Age of Genomics.* New York, NY: Columbia University Press, 58–81.

Lacy R.C. (2013) Achieving true sustainability of zoo populations. *Zoo Biology* 32: 19–26. doi: 10.1002/zoo.21029

Leader-Williams N., Harrison J., Green M.J.B. (1990) Designing protected areas to conserve natural resources. *Science Progress* 74: 189–204.

Lees C.M., Wilcken J. (2009) Sustaining the ark: the challenges faced by zoos in maintaining viable populations. *International Zoo Yearbook* 43: 6–18. doi: 10.1111/j.1748-1090.2008.00066.x

Leus K., Bingaman-Lackey L., van Lint W., de Man D., Riewald S., Veldkam A., Wijmans J. (2011) Sustainability of European Association of Zoos and Aquaria bird and mammal populations. *WAZA Magazine* 12: 11–14.

Lindburg D.G. (1991) Ecological requirements of macaques. *Laboratory Animal Science* 41: 315-322.

Lindburg D. (1992) Group size for captive lion-tailed macaques. *Lion-Tales* 8: 4–5.

Lindburg D.G., Iaderosa J., Gledhill L. (1997) Steady-state propagation of captive lion-tailed macaques in North American zoos: a conservation strategy. In: Walli, J. (ed). *Primate Conservation: The Role of Zoological Parks*. Chicago, Illinois: American Society of Primatologists, 131–149.

Lindburg D.G., Lasley B.L. (1985) Strategies for optimizing the reproductive potential of lion-tailed macaque colonies in captivity. In: Heltne, P. (ed). *The Lion-tailed Macaque: Status and Conservation.* New York, NY: Alan R. Liss, 343–356.

Łomnicki A. (1978) Individual differences between animals and the natural regulation of their numbers. *Journal of Animal Ecology* 47: 461–475.

Łomnicki A. (1988) Population ecology of individuals. Princeton, New Jersey: Princeton University Press.

Łomnicki A. (1999) Individual-based models and the individual-based approach to population ecology. *Ecological Modelling* 115: 191–198. doi: 10.1016/S0304-3800(98)00192-6

Long S., Dorsey C., Boyle P. (2011) Status of Association of Zoos and Aquariums cooperatively managed populations. *WAZA Magazine* 12: 15–18.

Lonsdorf E., Ross S.R. (2012) Socialization and development of behavior. In: Mitani, J., Call, J., Kappeler, P., Palombit, R.A. and Silk, J.B. (eds). *The Evolution of Primate Societies.* Chicago, Illinois: University of Chicago Press, 245–268. doi: 10.13140/2.1.4044.1284

Lott D.F. (1984) Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88: 266–325. doi: 10.1163/156853984X00353

Ludwig C., Dehnhard M., Pribbenow S., Silinski-Mehr S., Hofer H., Wachter B. (2019) Asymmetric reproductive aging in cheetah (*Acinonyx jubatus*) females in European zoos. *Journal of Zoo and Aquarium Research* 7: 87–93. doi: 10.19227/jzar.v7i2.382

Martin M.S., Shepherdson D.J. (2012) Role of familiarity and preference in reproductive success in ex situ breeding programmes. *Conservation Biology* 26: 649–656. doi: 10.1111/j.1523-1739.2012.01880.x.

Martin-Wintle M.S., Shepherdson D., Zhang G., Zhang H., Li D., Zhou X., Li R., Swaisgood, R.R. (2015) Free mate choice enhances conservation breeding in the endangered giant panda. *Nature Communications* 6. doi: 10.1038/ncomms10125.

Martin-Wintle M.S., Wintle N.J.P., Díez-León M., Swaisgood R.R., Asa C.S. (2019) Improving the sustainability of ex situ populations with mate choice. *Zoo Biology* 38: 119–132. doi: 10.1002/zoo.21450

Mason G., Burn C.C., Dallaire J.A., Kroshko J., Kinkaid H.M., Jeschke J.M. (2013) Plastic animals in cages: behavioural flexibility and responses to captivity. *Animal Behaviour* 85: 1113–1126. doi: 10.1016/j.anbehav.2013.02.002

McCann C., Powell D.M. (2019) Is there any more room on the ark? An analysis of space allocation in four mammalian taxa. *Zoo Biology* 38: 36–44. doi: 10.1002/zoo.21469

Mossotti R.H. (2010) Female Reaction to Male Urine Scents as a Potential Indicator of Mate Choice in Captive Cheetahs (*Acinonyx jubatus*). MSc thesis. Carbondale, Illinois: Southern Illinois University.

Norman A.J., Putnam A.S., Ivy J.A. (2019) Use of molecular data in zoo and aquarium collection management: benefits, challenges, and best practices. *Zoo Biology* 38: 106-118. doi: 10.1002/zoo.21451

Parker P.G., Waite T.A. (1997) Mating systems, effective population size, and conservation of natural populations. In: Clemmons, J.R. and Buchholtz, R. (eds). B*ehavioral Approaches to Conservation in the Wild.* Cambridge, UK: Cambridge University Press, 243–261.

Penfold L.M., Powell D., Traylor-Holzer K., Asa C.S. (2014) 'Use it or lose it': characterization, implications, and mitigation of female infertility in captive wildlife. *Zoo Biology* 33: 20–28. doi: 10.1002/zoo.21104

Powell D.M., Dorsey C.L., Faust L.J. (2019) Advancing the science behind animal program sustainability: an overview of the special issue. *Zoo Biology* 38: 5-11. doi: 10.1002/zoo.21474

Princée F.P.G. (2016) *Exploring Studbooks for Wildlife Management and Conservation*. Cham, Switzerland: Springer International Publishing.

Princée F.P.G., Glatston A.R. (2016) Influence of climate on the survivorship of neonatal red pandas in captivity. *Zoo Biology* 35: 104–110. doi: 10.1002/zoo.21266

Puurtinen M. (2011) Mate choice for optimal (K) inbreeding. *Evolution* 65: 1501–1505. doi: 10.1111/j.1558-5646.2010.01217.x

Ricklefs R.E. (1991) Structures and transformations of life histories*. Functional Ecology* 5: 174–183.

Roff D.A. (1992) *The Evolution of Life Histories: Theory and Analysis*. New York, NY: Chapman and Hall.

Sambatti J.B.M., Stahl E., Harrison S. (2008) Metapopulation structure and the conservation consequences of population fragmentation. In: Carroll, S.P. and Fox, C.W. (eds). *Conservation Biology: Evolution in Action.* New York, NY: Oxford University Press, 50–67.

Saunders S.P., Harris T., Traylor-Holzer K., Goodrowe-Beck K. (2014) Factors influencing breeding success, ovarian cyclicity, and cub survival in zoo-managed tigers. *Animal Reproductive Science* 14: 38–47. doi: 10.1016/j.anireprosci.2013.11.006

Schmidt P.M., Chakraborty P.K., Wildt D.E. (1983) Ovarian activity, circulating hormones and sexual behavior in the cat. II. Relationships during pregnancy, parturition, lactation and the postpartum estrus. *Biology of Reproduction* 28: 657–671. doi: 10.1095/biolreprod28.3.657

Schwitzer C., Kaumanns W. (2003) Foraging patterns of free-ranging and captive primates - implications for captive feeding regimes. In: Fidgett, A.L., Clauss, M., Gansloßer, U., Hatt, J-M. and Nijboer, J. (eds). *Zoo Animal Nutrition.* Fürth, Germany: Filander Verlag, 247–265.

Schwitzer C, Klumpe K, Kaumanns. 2002. Energy and nutrient intake, feeding behaviour and activity budget of captive douc langurs (*Pygathrix n. nemaeus*). In: Fidgett, A., Clauss, A., Eulenberger, K, Hatt, J.M., Hume, J., Janssens, G. and Nijboer, J. (eds). *Zoo Animal Nutrition* Vol III. Fürth, Germany: Filander Verlag, 109–124.

Sih A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour* 85: 1077–1088. doi: 10.1016/j.anbehav.2013.02.017

Sih A., Ferrari M.C.O., Harris D.J. (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications* 4: 367–387. doi: 10.1111/j.1752-4571.2010.00166.x

Singh M., Kaumanns W. (2005) Behavioural studies: a necessity for wildlife management. *Current Science* 89: 1230–1236.

Singh M., Kaumanns W., Singh M., Sushma H.S., Molur S. (2009) The lion-tailed macaque *Macaca silenus* (Primates: Cercopihecidae): conservation history and status of a flagship species of the tropical rainforests of the Western Ghats, India. *Journal of Threatened Taxa* 1: 151-157. doi: 10.11609/JoTT.o2000.151-7

Singh M., Kaumanns W., Umapathy G. (2012) Conservation-oriented captive breeding of primates in India: is there a perspective? *Current Science* 103: 1399–1400. doi: 10.11609/JoTT.o3625.4825-39

Singh M., Krishna B.A., Singh M. (2006) Dominance hierarchy and social grooming in female lion-tailed macaques (*Macaca silenus*) in the Western Ghats, India. *Journal of Biosciences* 31: 369–377. doi: 10.1007/BF02704110

Singh M., Kumara H.N., Kumar M.A., Sharma A.K. (2001) Behavioural responses of lion-tailed macaque to a changing habitat in a tropical rainforest fragment in Western Ghats, India. *Folia Primatologica* 72: 278–291. doi: 10.1159/000049949

Sinn D.L., Cawthen L., Jones S.M., Pukk C., Jones M.E. (2014) Boldness towards novelty and translocation success in captive-raised, orphaned Tasmanian devils. *Zoo Biology* 33: 36–48. doi: 10.1002/zoo.21108

Soulé M., Gilpin M., Conway W., Foose T. (1986) The millenium ark: how long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5: 101–113. doi: 10.1002/zoo.1430050205

Soulé M.E., Wilcox B.A. (eds) (1980) C*onservation Biology: An Evolutionary–Ecological Perspective.* Sunderland, Massachusetts: Sinauer Associates Inc.

Stearns S.C. (1976) Life-history tactics: a review of the ideas. *The Quarterly Review of Biology* 51: 3–47. doi: 10.1086/409052

Stearns S.C. (1992) *The Evolution of Life Histories*. Oxford, UK: Oxford University Press.

Stearns S.C. (2000) Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* 87: 476–486.

Stillman R.A., Railsback S.F., Giske J., Berger U., Grimm V. (2015) Making predictions in a changing world: the benefits of individual-based ecology. *BioScience* 65: 140–150. doi: 10.1093/biosci/biu192

Sugg D.W., Chesser R.K., Dobson F.S., Hoogland J.L. (1996) Population genetics meet behavioral ecology. *Trends in Ecology and Evolution* 11: 338–342. doi: 10.1016/0169-5347(96)20050-3

Swaisgood R.R., Schulte B.A. (2010) Applying knowledge of mammalian social organization, mating systems and communication to management. In: Kleiman, D.G., Thompson, K. and Kirk Baer, C. (eds). *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* 2nd Edition. Chicago, Illinois: The University of Chicago Press, 329–343.

Taborsky B., Arnold C., Junker J., Tschopp A. (2012) The early social environment affects social competence in a cooperative breeder. *Animal Behaviour* 83: 1067–1074. doi: 10.1016/j.anbehav.2012.01.037

Taborsky B., Oliveira R.F. (2012) Social competence: an evolutionary approach. *Trends in Ecology and Evolution* 27: 679–688. doi: 10.1016/j.tree.2012.09.003

Teitelbaum C.S., Converse S.J., Mueller T. (2017) Birds choose long-term partners years before breeding. *Animal Behaviour* 134: 147–154. doi: 10.1016/j.anbehav.2017.10.015

Thierry B., Singh M., Kaumanns W. (eds) (2004) *Macaque Societies: A Model for the Study of Social Organization.* Cambridge, UK: Cambridge University Press.

Thornton A., Clutton-Brock T. (2011) Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B Biological Sciences* 366: 978–987. doi: 10.1098/rstb.2010.0312

Traylor-Holzer K., Leus K., Bauman K.L. (2019) Integrated collection assessment and planning (ICAP) workshop: helping zoos move forward toward the one plan approach. *Zoo Biology* 38: 95–105.

Tuomainen U., Candolin U. (2011) Behavioural responses to human-induced environmental change. *Biological Reviews* 86: 640–657. doi: 10.1111/j.1469-185X.2010.00164.x

van Leeuwen E.J.C., Mulenga I.C., Chidester D.L. (2014) Early social deprivation negatively affects social skill acquisition in chimpanzees (*Pan troglodytes*). *Animal Cognition* 17: 407–414. doi: 10.1007/s10071-013-0672-5

Wachter B., Thalwitzer S., Hofer H., Lonzer J., Hildebrandt T.B., Hermes R. (2011) Reproductive history and absence of predators are important determinants of reproductive fitness: the cheetah controversy revisited. *Conservation Letters* 4: 47–54. doi: 10.1111/j.1755-263X.2010.00142.x

Walker S.E., Strasser M.E., Field L.P. (2004) Reproductive parameters and life-history variables in captive golden-bellied mangabeys (*Cercocebus agilis chrysogaster*). *American Journal of Primatology* 64: 123–131. doi: 10.1002/ajp.20066

Watters J.V. (2009) Toward a predictive theory for environmental enrichment. *Zoo Biology* 28: 609–622. doi: 10.1002/zoo.20284

Watters J.V., Bremner-Harrison S., Powell D.M. (2017) Phenotype management: an inclusive framework for supporting individuals' contributions to conservation populations. In: Vonk, J., Weiss, A. and Kuczaj, S.A. (eds). *Personality in Nonhuman Animals.* Cham, Switzerland: Springer International Publishing, 277–294.

Watters J.V., Lema S.C., Nevitt G.A. (2003) Phenotype management: a new approach to habitat restoration. *Biological Conservation* 112: 435–445. doi: org/10.1016/S0006-3207(02)00343-9

Watters J.V., Meehan C.L. (2007) Different strokes: can managing behavioral types increase post-release success? *Applied Animal Behaviour Science* 102: 364–379. doi: 10.1016/j.applanim.2006.05.036

Wielebnowski N.C., Ziegler K., Wildt D.E., Lukas J., Brown J.L. (2002). Impact of social management on reproductive, adrenal and behavioural activity in the cheetah (*Acinonyx jubatus*). *Animal Conservation* 5: 291–301. doi: 10.1017/S1367943002004043

Williams S.E., Hoffman E.A. (2009) Minimizing genetic adaptation in captive breeding programs: a review. *Biological Conservation* 142: 2388–2400. doi: 10.1016/j.biocon.2009.05.034

Zinner D., Hindahl J., Kaumanns W. (2001) Experimental intergroup encounters in lion-tailed macaques (*Macaca silenus*) *Primate Report* 59: 77–92.

Chapter 6: General Discussion

Some of the captive populations of wild animals in zoos are supposed to support the conservation of species by serving as reserves, models, and resources for research and conservation education. Breeding programmes were established to realise these aims. Many of the populations in zoos, however, are not doing well; the potential to develop towards sustainability seems to be low (Che-Castaldo et al. 2019). The captive population of the lion-tailed macaque *Macaca silenus* is one of the oldest primate populations in zoos. The wild population is threatened due to fragmentation, alteration of its habitat, and local hunting. The captive population suffers from low population growth. Breeding problems are reported since decades.

Our study intended to analyse the development and conservation potential of the population on different levels. For the first time, the complete history and development of the global population over more than 100 years were traced. As a key aspect, the individual patterns of reproduction were analysed. The influences on the patterning of reproduction by the types of groups in which the individuals were kept, and various other management measures were assessed.

The study refers to the *complete* historical captive population of the species, including thousands of individuals in hundreds of zoos over a long time period allowing the emergence of minimally eight generations. Its results provide valuable information for the further management of the living population. The long-term persistence of captive populations is a key aspect for their value as a reserve and one of the key topics of conservation and zoo biology. The captive population of the lion-tailed macaque with studbook data on all members of the population over a hundred years is of special value there. They allow us to establish a differentiated picture on various levels like time periods, subpopulations, locations, and groups, respectively, and their importance and influences on the long-term development of the population. The contribution of individual females and males to the patterns of reproduction in the population is of utmost importance there. Especially, knowledge about the reproductive output of the individuals of a population over long periods, allows the assessment of the reproductive potential and, therefore, also the conservation potential of the population.

6.1 Population development and history

Chapter 2 – The population revealed a potential to persist over decades under highly dispersed conditions and an overall heterogeneous management; local management of individual zoos played a dominant role (see also Lindburg and Forney 1992).

The population increased in size slowly but steadily for about sixty years of its existence without the further import of animals from the wild. A decrease in size was management-induced from 1994 to 2000 and from 2012 onward via birth control and removal of individuals. The population increased in size, although only 40% of the females contributed to reproduction. The number of births was overall only slightly higher than the number of deaths. This and the overall high infant mortality kept the population in a fragile status. The two large subpopulations (North America and Europe) that mainly constituted the population developed similarly over two decades before the management of the American population led to a decrease in population size and productivity there. In North America, the management emphasised genetic aspects and the use of "hedge-breeding". The latter assumed that a small number of genetically defined individuals could be established as a reserve that could be activated when needed. The main reason behind this "policy" was a lack of holding spaces in zoos. Holding spaces for lion-tailed macaques were competing with spaces for other species. The "space problem" was not discussed under the requirements resulting from the reproductive and social system of the species. The implementation of the hedge-breeding was not successful and led to a number of logistical problems, a loss of interest and finally to a small ageing non-breeding stock. Another reason for a loss of interest was the occurrence of Herpes B infections in some macaque species housed in biomedical facilities, although no cases of human infections were documented from zoos (see Lindburg 1993; Ness 2013). Space problems similarly emerged in the European population two decades later. From the management of spaces, as carried out in the global captive population of the lion-tailed macaque, it can be learnt that it plays an important role for the survival of a population. The available space has to allow the functioning of the reproductive and social system of a species.

The changes in terms of population size and breeding policy in North America, as carried out in the context of space management, were not discussed on the level of the global population. The negative consequences for the latter (see below) demonstrate the need for global management. An international discussion about relevant aspects of the biology of the species and the integration of new information from the wild population and other captive populations was missing. The use of adaptive management (Walters and Hilborn 1978), with its recommended checks on the effects of management measures, would have prevented losses in terms of phenotypic diversity and would have prevented the dissolution of important parts of the global population.

6.2 Patterns of reproduction

In **Chapter 3** the study also looks *behind* the overall development of the global historical captive population of the lion-tailed macaque in order to assess its potential for long-term persistence. It focuses on the investigation of the patterns of reproduction in terms of individual reproductive output and the distribution of group sizes over the full period of the existence of the global historical captive population. The study identifies alterations in living conditions that might establish mismatches with species-typical adaptations and potentially influence the productivity of the population.

It was expected that the productivity of the population would be low. The results of our study support these assumptions: a large proportion of the females did not breed at all. Those who bred revealed large individual differences. Only about 24% of the males bred at all. Infant mortality was high, constituting a large proportion of overall mortality (see also Chapter 2). This patterning characterises the population over its full history (Lindburg 1980; Kaumanns and Rohrhuber 1995; Kaumanns et al. 2013). In both the big subpopulations (North America and Europe), the development was influenced temporarily by birth control measures on a large scale. They added to low productivity. The number of infants per adult female in periods of birth control was lower than that during the programme periods without birth control. It was also lower than during periods with no systematic management.

The study reveals that the patterns of reproduction and basic aspects of the living conditions do not correspond to those in the wild and induce mismatches with species-typical adaptations, in particular, a life in a female bonded system. The emergence of mismatches was also supported by a distribution of group sizes with overall small numbers of individuals per location. Small groups revealed lowest numbers of infants per breeding female. Most individuals of the population had to live under suboptimal, demographic, and possibly resulting social conditions. Frequent transfers of females between groups contributed to mismatches. “Female dispersal” is not found in the wild population; females remain in their natal groups lifelong. The number of infants per adult female was higher in females that remained in their natal groups than those that were transferred to new groups. Mismatches were also induced by the altered and artificial living conditions in zoos. Groups in zoos were usually fully isolated (“fragmentation”).

Some results on the captive population revealed similarities with observations on wild lion-tailed macaques living in degraded, isolated forest fragments where the reproductive output is found to be lower than in contiguous forests (Kumar 1995). In smaller fragments, the reproductive output is lower than in larger fragments (Umapathy and Kumar 2000, 2003).

The captive population of the lion-tailed macaque, despite a low mean reproductive output per female, survived over several decades without further input from the wild, however, resulting in a fragile status of the current population. In terms of efficiency as a breeding device and a potential reserve, the results are suboptimal: the breeding potential of a large proportion of the individuals of the population, especially of the females and of the males, was not used. Infant mortality was high. An enormous loss of phenotypic and genetic diversity is likely.

Since the current captive population still constitutes about 11% of the total population, it is evident that the remaining number of individuals in the captive population is important for the future of the conservation of the species. An adaptive management, as mentioned above, would have had to consider the potential long-term consequences of poor breeding in the individual groups for the persistence of the population. The reproductive and social systems should have been considered more strongly in management plans. Low reproductive output as known prior to the implementation of birth control, was not addressed as suggested by the declining population paradigm (*sensu* Caughley 1994). Global management plans should have declared the investigation of the reasons for breeding problems as a key goal of the programme like it was done temporarily in the European breeding programme (1989–2006; see Kaumanns et al. 2013). Only a certain proportion of the females breed successfully during all periods in the history of the population. Whenever breeding was propagated, the number of births and population size increased – in North America, since about a decade before the programme started, in Europe with the establishment of the programme. Space problems emerged sooner in North America and later in Europe, leading to “invasive” measures including birth control and removal of individuals. The attention was focused on the space problems. In both subpopulations, birth control measures were initiated when population size and the number of births peaked. Positive developments, as reflected in higher numbers of births, were interrupted. The possibly still existing breeding problems in many females were no more considered. The consequences for the long-term development of the breeding potential of the females and the population, respectively, were not fully considered. Birth and population size control helped to reduce the space problems but possibly reduced the breeding potential and the chances for the population to survive (see the example of the North American population). Later efforts to restart breeding in selected zoos did not succeed (see Carter and Ness 2012). For the negative consequences of periods of non-breeding on the physiological status of the females, see Penfold et al. (2014).

The reproductive system of the species, like in other macaque species, is realised in a social system that has permanent bonds between related females that stay lifelong in their natal groups. This female-bonded system is regarded as a key-trait of the species (*sensu* Carroll and Watters 2008) that should guide management. It is a condition for successful breeding. Low breeding in the global captive population might be mainly a consequence of inappropriate management that did not consider enough the female-bonded social system of the species. A number of authors point to breeding and sustainability problems in zoo-kept elephants (Wiese 2000; Rees 2003; Wiese and Willis 2006). Schulte (2000), Clubb and Mason (2002), Rees (2009), and Prado-Oviedo et al. (2016) describe deviations in the demographic and social conditions elephants in zoos are confronted with in comparison to the conditions in the wild. The recently edited "Best Practice Guidelines" of the EAZA propagate improvements in husbandry practices, most importantly keeping elephants in species-typical social units that consist of a matriarch, her daughters, and their offspring (Schmidt and Kappelhof 2019).

More generally, the study in chapter 3 proposes that to save the future of the captive population of the lion-tailed macaque, in addition to improved management and husbandry practice, a new international population management approach is needed. It should more consequently consider relevant concepts of evolutionary biology and, in particular life-history theory (see Chapter 5).

6.3 Future of the lion-tailed macaque – Management considerations

Chapter 4 mainly considers the conservation of the endangered lion-tailed macaque with reference to the potential contribution of the global captive population. The paper was written in the context of the re-establishment of the international studbook. The perspectives it proposes are based on the most recent status of the global captive population of the lion-tailed macaque. It is especially addressed to professionals involved in decision-making and organising conservation activities. It intended to provide a short overview of the status and management history of the global historical captive population with special reference to the current population, a main part of which is kept in Europe. In particular, the role of the Indian population for the conservation of the species is considered. Large Indian zoos can provide the spaces that are needed to allow European and other groups of lion-tailed macaques to grow and contribute to the establishment of a larger and viable population. Indian zoos still keep a few wild-born individuals that could improve the genetic status of the global population. A special role of the Indian zoo community and conservation organisations within an *in situ – ex situ*/ one-plan approach is put forward. The plan should mainly be realised within an "Indo-European lion-tailed macaque reserve population" project constituted by members of zoos and their organisations, researchers from conservation-oriented research institutions, and other experts from India and Europe. An integrated *in situ – ex situ/* one-plan approach is necessary. It should strongly refer to the complete global captive population and manage it as a metapopulation following the principles of adaptive management. The core of the population would be the European, Indian, and Japanese subpopulations.

It should include:

- International conservation-oriented research projects including field studies.
- The establishment of appropriate infrastructural conditions in selected Indian zoos for breeding lion-tailed macaques and possibly for their reintroduction in the wild.
- Improving infrastructural conditions should also include the training of experts, from the level of keepers to zoo biologists/curators.
- Both Indian research institutions and selected zoos should serve as interfaces to the wild population.
- The establishment of an international board of experts to guide and supervise the project is of utmost importance

The work could be based on the efforts and structures discussed in various symposia and congresses from 1980 to 2003 (Heltne 1985; Melnick 1990; Kumar et al. 1995b; Schwibbe et al. 2000, 2001; Molur et al. 2003). A revival of interest in captive propagation and *in situ – ex situ* conservation-oriented programmes have to be stimulated in India. A critical point for the management of the captive population emerged with the findings of two genetically different subpopulations in the Western Ghats (Ram et al. 2015). Whether specimens of the different types have to be managed separately is under discussion. Separate management in the zoo populations would have to be based on large-scale testing and possibly require new management approaches. This is of special importance for the European captive population which constitutes 62% of the current global population.

6.4 Conceptual considerations for the management of captive populations – Animals are designed for breeding

Chapter 5 is of a general nature and does not specifically refer to the study population. It rather refers to the viability and sustainability problems the management of captive populations of birds and mammals are facing. The investigation of the development and the patterns of reproduction of the captive population of the lion-tailed macaque also reveals corresponding problems.

The sustainability and long-term persistence of threatened populations of wild and captive animals is a dominant topic of conservation and zoo biology, respectively. Breeding problems are a main cause of sustainability problems in many species in zoos. Many recent studies reveal that a large proportion of the captive populations will not persist in the long run. One of the important goals of zoos in terms of providing reserve populations cannot be realised sufficiently. There are efforts to improve the situation (Powell et al. 2019), but the development of many populations is not promising. The paper presented (Chapter 5) starts from the assumption that small-scale improvements, as realised since years, or proposed, for instance, by Powell et al. (2019), will not lead to significant changes. A change in management paradigm is required. Following Caughley (1994), the threatened status of most populations suggests a switch from the so far used “small population paradigm” in population management in zoos with its emphasis on genetic aspects to the “declining population paradigm”. This approach emphasises the need to elaborate on the causes for the sustainability problems. The flowchart (Figure 2) below provides an overview of the two approaches. It roughly points to the concepts used by zoo biologists and population managers following the small population paradigm. Here, the unit of management is the population and its genetic structure. The individuals of a population are mainly regarded under the perspective of their genotypes. The goal of population management is to preserve genetic diversity; individuals should transfer their “genetic raw material” to the next generations.

The declining population paradigm recommends searching for the causes of the decline of a population. In accordance with this, the manuscript (chapter 5) reconsiders the conceptual background of gene-biased population management as described above. It is emphasised to refer more consequently to evolutionary biology and, in particular, life-history theory. The approach focuses on the individual phenotype as a whole. The goal of population management is to produce adapted phenotypes and populations. Individuals should be able to breed successfully and transfer their genotypes and phenotypes to the next generation. Breeding should be performed in a species-typical way, and the potential to do so should be preserved. To achieve this, the key-traits of a species need to be considered. Aspects of the theoretical background and the main components of the proposed management approach are presented in Figure 2.

The theoretical aspects and background of the approach of the paper, as presented in Figure 2, are not discussed further here. Some of its consequences for the practical management of captive populations, especially mammal populations, are rather briefly elaborated by using examples.

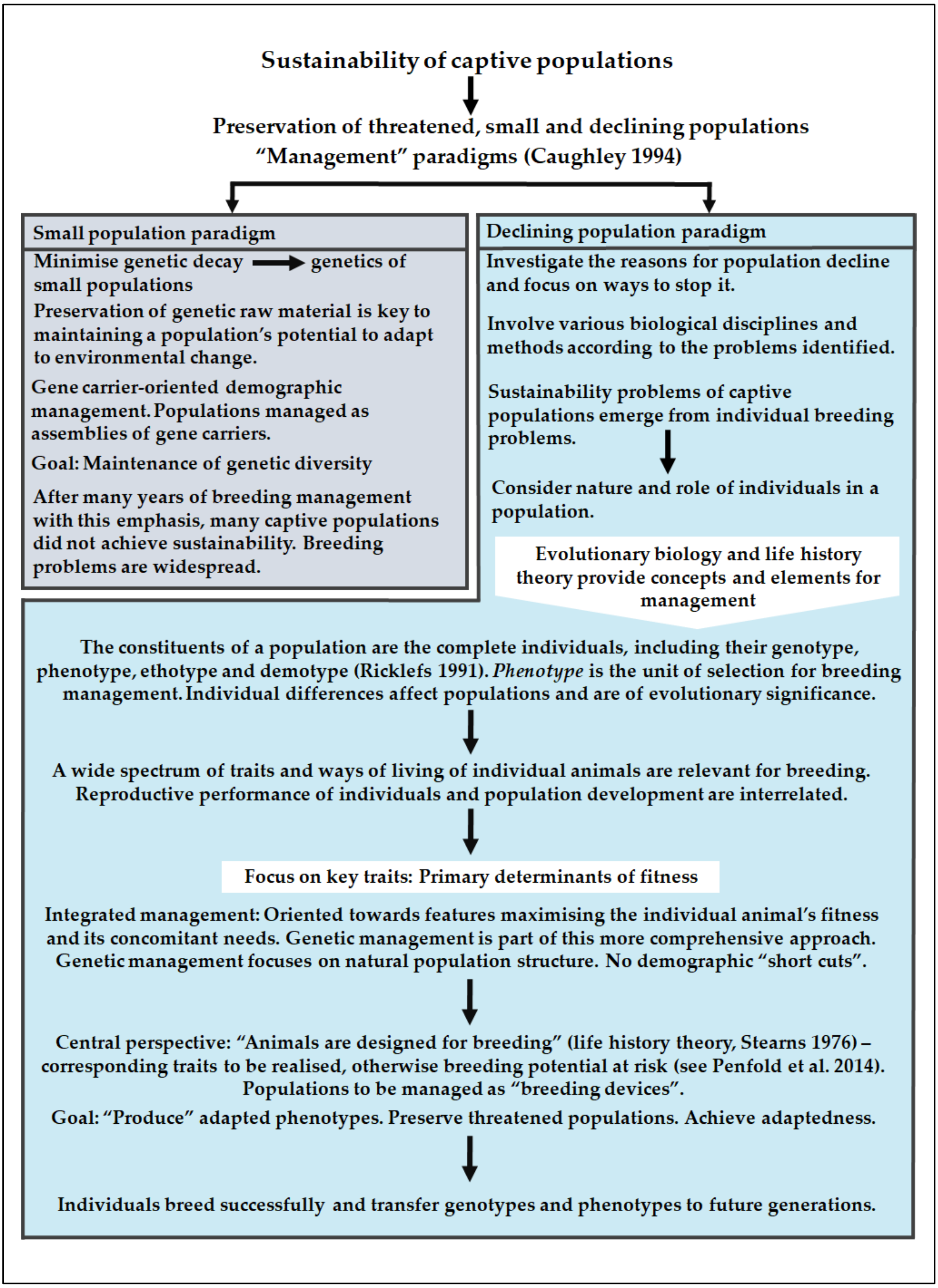
The main perspective of management plans should be to achieve the persistence of a population by treating it consequently as a breeding device. Kaumanns and Singh (2015) proposed putting emphasis on individuals as units of reproduction and considering their individual life histories and roles within a population. Following life-history theory, the various levels (genotype, phenotype, ethotype, i.e., behaviour and physiological processes, and demotype, i.e., age-specific fecundity and survival value) of an individual should be considered equally important for fitness maximisation and thus for management. For example, the behavioural skills of a primate female should be considered in the context of infant rearing. Her experience and skills are as relevant as her genetic status to reproductive success and recruitment for population management. Management has to provide the appropriate conditions for acquiring these skills. This might include the presence of mothers, aunts, or other group members and appropriate group size and composition. This is also important for the socialisation of males. This is not restricted to primates. It is also important for other species with complex societies, such as elephants and spotted hyenas (*Crocuta crocuta*, Hofer and East 2003).

Population management for the lion-tailed macaque and other mammals would require knowledge about the (reproductive) biology of the species and information about the individuals, especially about the females. Living and especially breeding conditions should be designed such that the reproductive system can function optimally. Goal should be not only to produce infants but preserve the potential to do so especially considering the altered conditions in zoos. Captive populations that are temporarily or partly restrained from reproducing are likely to lose their breeding potential. For the lion-tailed macaque, for instance, a life in a female-bonded system is regarded as a - directly fitness relevant - key trait, within which reproduction takes place. The conditions for the existence and functioning of a female-bonded system are complex. Management and husbandry systems have to consider the group size and composition. A group should minimally have a cluster of related females as a permanent core and a properly socialised breeding male. Breeding males should be exchanged periodically, with appropriate integration procedures. Groups should be allowed to grow such that generational overlap is induced. The natural habitat of the species reveals an arboreal way of living, allowing large individual distances. This requires very spacious enclosures with structures functionally equivalent to canopy structures. The enclosures should also allow the patterns of spacing typically needed in the context of consort pairing and female-female competition about the adult male.

The proposed individual-based management has to consider genetic aspects but has to balance them against the need to consider traits that require behavioural skills and social competence.

An integrated management approach with emphasis on breeding will lead to more productive and larger populations but also to space problems. How to deal with “surplus individuals”, that is, with animals that in the wild would be part of the food chain, is a pending problem for population management. The role of euthanasia has to be seriously considered.

Overall, the development of more flexible housing systems, that incorporate the essentials of a species’ niche or habitat is required.



Sustainability of captive populations

Preservation of threatened, small and declining populations
"Management" paradigms (Caughley 1994)

Small population paradigm

Minimise genetic decay → genetics of small populations

Preservation of genetic raw material is key to maintaining a population's potential to adapt to environmental change.

Gene carrier-oriented demographic management. Populations managed as assemblies of gene carriers.

Goal: Maintenance of genetic diversity

After many years of breeding management with this emphasis, many captive populations did not achieve sustainability. Breeding problems are widespread.

Declining population paradigm

Investigate the reasons for population decline and focus on ways to stop it.

Involve various biological disciplines and methods according to the problems identified.

Sustainability problems of captive populations emerge from individual breeding problems.

Consider nature and role of individuals in a population.

Evolutionary biology and life history theory provide concepts and elements for management

The constituents of a population are the complete individuals, including their genotype, phenotype, ethotype and demotype (Ricklefs 1991). *Phenotype* is the unit of selection for breeding management. Individual differences affect populations and are of evolutionary significance.

A wide spectrum of traits and ways of living of individual animals are relevant for breeding. Reproductive performance of individuals and population development are interrelated.

Focus on key traits: Primary determinants of fitness

Integrated management: Oriented towards features maximising the individual animal's fitness and its concomitant needs. Genetic management is part of this more comprehensive approach. Genetic management focuses on natural population structure. No demographic "short cuts".

Central perspective: "Animals are designed for breeding" (life history theory, Stearns 1976) – corresponding traits to be realised, otherwise breeding potential at risk (see Penfold et al. 2014). Populations to be managed as "breeding devices".

Goal: "Produce" adapted phenotypes. Preserve threatened populations. Achieve adaptedness.

Individuals breed successfully and transfer genotypes and phenotypes to future generations.

Figure 2. Flowchart of the approach

6.5 Database/Methods – The international studbook for the lion-tailed macaque and methods

Individuals in captive populations foreseen as reserves should remain genetically and phenotypically close to their wild conspecifics. The population should persist over long time periods. Corresponding population management is required. It has to be based on the concepts of a number of biological disciplines and know-how on the practicalities of population management and husbandry. Population management is based on records of the individuals of the population and their living conditions. Individual records for a captive population of a species are provided by national and international studbooks only. They provide materials to support decision-making and management plans for the populations in question. They are established by studbook keepers who compile the information provided by individual zoos. Although the collection of individual data and its use for management purposes have been improved through the use of computers and special software since the 1980s, information recorded in zoos in earlier decades was often poor and difficult to access. The studbooks usually contain only individual records, including individual identification, sex, origin, parentage when known, locations and dates of births, transfers, and deaths. Further information, for instance, about living conditions and husbandry styles, is usually available in additional publications only – if at all.

Our study is based on the international studbook of the lion-tailed macaque (Sliwa and Begum 2019). International and regional studbooks of the species were first established in the 1980s. They belonged to some of the first studbooks for primates. The founding studbook keeper Laurence Gledhill in the 1980s, had to trace data back to over almost a hundred years, being confronted with poor local records established in times with different husbandry, philosophies, and approaches of zoos. The current international studbook as of, 2019, provides the resulting information and, like several regional versions, experienced updates and corrections over the decades. The first edition of the international studbook covered a period of 87 years and included a total of 1,044 animals (Gledhill 1987), and the latest published edition contains information on 2,734 individuals covering a period of 119 years from 1899 to 2018 (Sliwa and Begum 2019).

Since a population is constituted by its individuals, the analysis of the development and conservation potential of a population has to start from the individuals (Chapter 5; Kaumanns and Singh 2015). The analysis of the history and development of the global historical population of the lion-tailed macaque has to be based on individual records. Updated individual records have been compiled for the current studbook and used in the study. The study of a social species like the lion-tailed macaque, however, would require information about its living and especially social living conditions. Our study has to deal with a lack of direct information there and concludes from the information about the locations of individuals as given in the studbook to the existence of groups. Conclusions about the quality of these "groups" allow an assessment of their potential as species-typical breeding units. The results on the distribution of group sizes reveal a predominance of small sizes. The data, although rough and simple, reliably note that the overall demographic conditions of the lion-tailed macaques in the population deviate from the ones in the wild.

A lack of information on the living conditions (enclosures) and social conditions of individuals and groups is a typical problem population analysis and management are confronted with. Our study proposes a means to deal with it. Though there are efforts of zoo biologists to improve data management, including more information on social living conditions (e.g., ZIMS), the limited potential and poor quality of data older than 50 years remain. However, the usually reliable studbook data on individual history records can often compensate for a lack of corresponding data from field studies (see Princée 2016). In the case of the lion-tailed macaque, for instance, long-term studies on the patterning of reproduction on the population level in the wild are missing.

The predominately descriptive approach of our study and the nature of the data as provided by the studbook limit the potential of the study to use inferential statistics. For instance, the distribution of group sizes as assessed from the number of individuals per location can allow hints on the overall demographic structure and the resulting reproductive potential of the population. It is evident, however, that the latter is influenced by more factors than "group size", for instance, by enclosures, food, health conditions, husbandry systems, and approaches of zoos toward conservation and welfare. An influence of these factors on the chances of a female to reproduce is likely but cannot be deduced from the studbook records.

The limits of studbook data in terms of information about living conditions and management procedures are evident. They are, however, the only long-term data available to trace aspects of the development of a captive population. They, therefore, are essential for the establishment or improvement of population management programmes. For the value of individual-based long-term studies and their importance for future research projects with new research questions, see Clutton-Brock and Sheldon (2010) and Sheldon et al. (2022).

Conclusions

Since the 1980s, the work with captive populations in zoos has been conservation-oriented. Besides an important role in educating the public about the need to conserve nature, captive populations were expected to function as reserves and resources for research for their threatened wild conspecifics. This was also proposed for the lion-tailed macaques in zoos (Heltne 1985; Conway 1985). Our study indicates some potential of the captive population as a reserve: after an initial period based on wild-caught individuals, it persisted over decades via breeding and without the integration of wild-born animals. The establishment of breeding programmes supported population growth but also initiated maladaptive developments. Overall, under the perspective of the population as a breeding device, breeding efficiency was low. About 40% of the females and 24% of the males in the population contributed to reproduction. It is likely that there was an enormous loss of phenotypic and genetic diversity. Many potential founders and breeders were "wasted". Our study identifies mismatches, especially in the context of demography and social life, that might have contributed to this. Concluding from the developmental trends as described in our study, the breeding programmes, with their current structures and management activities, are not likely to support the persistence of the lion-tailed macaque population. A new global management approach based on an international working unit with a central role of scientists of the country of origin is needed. Already existing *in situ – ex situ* links and cooperations need to be emphasised. Management and husbandry programmes themselves have to be based more strongly on the biology of the species and focus on the individuals. Important aspects are elaborated and discussed in the study. Under the perspective of the conservation of an endangered species, the persistence of the captive population of the lion-tailed macaque is a value *per se*. It is one of the oldest, largest, and best studied primate populations; its value as a model and resource for research also needs to be considered more strongly.

References for summary, general introduction, and general discussion

Abegg C, Thierry B. 2002. Macaque evolution and dispersal in insular south-east Asia. Biological Journal of the Linnean Society 75: 555–576.

Allee WC. 1931. Animal Aggregations: A study in General Sociology. University of Chicago Press.

Anandam MV, et al. 2013. Family Cercopithecidae (Old World monkeys) – Species accounts of Cercopithecidae. Pages 628–753 in Mittermeier RA, Rylands AB, Wilson DE, eds. Handbook of the Mammals of the World, vol. 3, Primates. Lynx Edicions.

Anthony LL, Blumstein DT. 2000. Integrating behaviour into wildlife conservation: The multiple ways that behaviour can reduce Ne. Biological Conservation 95: 303–315.

Armstrong DP. 2005. Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. Conservation Biology 19: 1402–1410.

Armstrong DP, Seddon PJ. 2008. Directions in reintroduction biology. Trends in Ecology and Evolution 23: 20–25.

Arroyo-Rodriguez V, Dias PAD. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: A review. American Journal of Primatology 72: 1–16.

Asquith NM. 2001. Misdirections in conservation biology. Conservation Biology 15: 345–352.

Baker A. 2007. Animal ambassadors: An analysis of the effectiveness and conservation impact of *ex situ* breeding efforts. Pages 139–154 in Zimmerman A, Hatchwell M, Dickie LA, West C, eds. Zoos in the 21st Century: Catalysts for Conservation? Cambridge University Press.

Ballou JD, Lacy RC. 1995. Identifying genetically important individuals for management of genetic diversity in pedigreed populations. Pages 76–111 in Ballou JD, Gilpin M, Foose TJ, eds. Population Management for Survival & Recovery. Analytical Methods and Strategies in Small Population Conservation. Columbia University Press.

Ballou JD, Traylor-Holzer K. 2011. Captive populations and genetic sustainability. WAZA Magazine 12: 19–22.

Ballou JD, Kleiman DG, Mallinson JJC, Rylands AB, Valladares-Padua CB, Leus K. 2002. History, management and conservation role of the captive lion tamarin populations. Pages 95–114 in Kleiman DG, and Rylands AB, eds. Lion Tamarins: Biology and Conservation. Smithsonian Institution Press.

Ballou JD, Lees C, Faust LJ, Long S, Lynch C, Lackey LB, Foose TJ. 2010. Demographic and genetic management of captive populations. Pages 219–252 in Kleiman DG, Thompson K, Baer CK, eds. Wild Mammals in Captivity: Principles and Techniques For Zoo Management. 2nd ed. The University of Chicago Press.

Ballou JD, Lacy RC, Pollak JP. 2022. PMx: Software for demographic and genetic analysis and management of pedigreed populations (Version 1.6.5.20220325). Chicago Zoological Society. (29 December 2022; www.scti.tools)

Balmford A, Kroshko J, Leader-Williams N, Mason G. 2011. Zoos and captive breeding. Science 332: 1149–1150.

Barlow SC, Hibbard C. 2005. Going, Going, Gone. A Zoo Without Exotic Mammals? ARAZPA Submission 148b. Department of Agriculture, Fisheries and Forestry, Canberra.

Bassett L, Buchanan-Smith HM. 2007. Effects of predictability on the welfare of captive animals. Applied Animal Behaviour Science 102: 223–245.

Beck BB, Rapaport LG, Stanley Price MS, Wilson AC. 1994. Reintroduction of captive born animals. Pages 256–286 in Olney PJS, Mace GM, Feistner ATC, eds. Creative Conservation: Interactive Management of Wild and Captive Animals. Chapman and Hall.

Bolam FC, et al. 2021. How many bird and mammal extinctions has recent conservation action prevented? Conservation Letters 14: e12762.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: Incidence and implications of individual specialization. The American Naturalist 161: 1–28.

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur D. 2011. Why intraspecific trait variation matters in ecology. Trends in Ecology and Evolution 26: 183–192.

Boyce MS. 2002. Reconciling the small-population and declining-population paradigms. Pages 41–49 in Beissinger SR, McCullough DR, eds. Population Viability Analysis. Chicago University Press.

Brambell FWR. 1965. Report of the Technical Committee to Enquire into the Welfare of Animals kept under Intensive Livestock Husbandry Systems. (Command Rep. 2836). Her Majesty's Stationery Office, London.

Brichieri-Colombi TA, Lloyd NA, McPherson JM, Moehrenschlager A. 2019. Limited contributions of released animals from zoos to North American conservation translocations. Conservation Biology 33: 33–39.

Brook BW, Bradshaw CJA, Traill LW, Frankham R. 2011. Minimum viable population size: Not magic, but necessary. Trends in Ecology & Evolution 26: 619–620.

Broom DM, Johnson KG. 2019. Stress and Animal Welfare. 2nd ed. Springer.

Brown JL, Olson D, Keele M, Freeman EW. 2004. Survey of the reproductive cyclicity status of Asian and African Elephants in North America. Zoo Biology 23: 309–321.

Brown JL, Paris S, Prado-Oviedo NA, Meehan CL, Hogan JN, Morfeld K, Carlstead K. 2016. Reproductive health assessment of female elephants in North American zoos and association of husbandry practices with reproductive dysfunction in African elephants (*Loxodonta africana*). PLOS ONE 11: e0145673.

Byers O, Lees C, Wilcken J, Schwitzer C. 2013. The one plan approach: The philosophy and implementation of CBSG’s approach to integrated species conservation planning. WAZA Magazine 14: 2–5.

Carlstead K. 1996. Effects of captivity on the behavior of wild mammals. Pages 317–333 in Kleiman DG, Allen ME, Thompson KV, Lumpkin S, Harris H, eds. Wild Mammals in Captivity: Principles and Techniques for Zoo Management. 1st ed. The University of Chicago Press.

Caro TM, Laurenson MK. 1994. Ecological and genetic factors in conservation: A cautionary tale. Science 263: 485–486.

Carroll SP, Watters JV. 2008. Managing phenotypic variability with genetic and environmental heterogeneity: Adaptation as a first principle of conservation practice. Pages 183–200 in Carroll SP, Fox CW, eds. Conservation Biology: Evolution in Action. Oxford University

Press.

Carter S, Ness T. 2012. Population Analysis & Breeding and Transfer Plan Lion-tailed Macaque (*Macaca silenus*) AZA Species Survival Plan Yellow Program. Minnesota Zoo, Minnesota, and Association of Zoos and Aquariums (AZA), Silver Spring, Maryland.

Caughley G. 1994. Directions in conservation biology. The Journal of Animal Ecology 63: 215–244.

Caughley G, Gunn A. 1996. Conservation Biology in Theory and Practice. Blackwell Science.

Chandran MDS. 1997. On the ecological history of the Western Ghats. Current Science 73: 146–155.

Chapman CA, Omeja PA, Kalbitzer U, Fan P, Lawes MJ. 2018. Restoration provides hope for faunal recovery: Changes in primate abundance over 45 years in Kibale National Park, Uganda. Tropical Conservation Science 11: 1–5.

Chargé R, Teplitsky C, Sorci G, Low M. 2014. Can sexual selection theory inform genetic management of captive populations? A review. Evolutionary Applications 7: 1120–1133.

Che-Castaldo J, Johnson B, Magrisso N, Mechak L, Melton K, Mucha K, Terwilliger L, Theis M, Long S, Faust L. 2019. Patterns in the long-term viability of North American zoo populations. Zoo Biology 38: 78–94.

Chrulew M. 2018. My place, my duty: Zoo biology as field philosophy in the work of Heini Hediger. Parallax 24: 480–500.

Chrulew M. 2020. Reconstructing the worlds of wildlife: Uexküll, Hediger, and beyond. Biosemiotics 13: 137–149

Clarke AS, Harvey NC, Lindburg DG.1992. Reproductive coordination in a nonseasonally breeding primate, *Macaca silenus*. Ethology 91: 46–58

Clubb R, Mason G. 2002. A Review of the Welfare of Zoo Elephants in Europe. Report commissioned by the RSPCA. Animal Behaviour Research Group, University of Oxford.

Clutton-Brock TH, Sheldon BC. 2010. Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology and Evolution 25: 562–573.

Coe J, Dykstra G. 2010. New and sustainable directions in zoo exhibit design. Pages 202–215 in Kleiman DG, Thompson KV, and Kirk Baer C, eds. Wild Mammals in Captivity: Principles and Techniques for Zoo Management, 2nd ed. The University of Chicago Press.

Conde DA, Flesness N, Colchero F, Jones OR, Scheuerlein A. 2011a. An emerging role of zoos to conserve biodiversity. Science 331: 1390–1392.

Conde DA, Flesness N, Cochero F, Jones OR, Scheuerlein A. 2011b. Zoos and captive breeding – response. Science 332: 1150–1151.

Conde DA, Colchero F, Gusset M, Pearce-Kelly P, Byers O, Flesness N, Browne RK, Jones OR. 2013. Zoos through the lens of the IUCN red list: A global metapopulation approach to support conservation breeding programs. PLOS ONE 8: e80311.

Conway W. 1985. Saving the lion-tailed macaque. Pages 1–12 in Heltne PG, ed. The Lion-tailed Macaque: Status and Conservation. Monographs in Primatology, vol. 7. Alan R. Liss.

Conway W. 1995. Wild and zoo animal interactive and habitat conservation. Biodiversity and Conservation 4: 573–594.

Conway WG. 2011. Buying time for wild animals with zoos. Zoo Biology 30: 1–8.

Crandall LS. 1964. The Management of Wild Mammals in Captivity. The University of Chicago Press.

Courchamp F, Berec L, Gascoigne J. 2008. Allee Effects in Ecology and Conservation. Oxford University Press.

Daigle CL, Brown JL, Carlstead K, Pukazhenthi B, Freeman EW, Snider RJ. 2015. Multi-institutional survey of social, management, husbandry and environmental factors for the SSP African lion *Panthera leo* population: Examining the effects of a breeding moratorium in relation to reproductive success. International Zoo Yearbook 49: 198–213.

Dall SR, Bell AM, Bolnick DI, Ratnieks FL. 2012. An evolutionary ecology of individual differences. Ecology Letters 15: 1189–1198.

Darwin C. 1859. On the Origin of Species by Means of Natural Selection. John Murray.

Dawkins MS. 1980. Animal Suffering. Chapman and Hall.

de Almeida-Rochaa JM, Peres CA, Oliveira LC. 2017. Primate responses to anthropogenic habitat disturbance: A pantropical meta-analysis. Biological Conservation 215: 30–38

Delson E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment. Pages 10–30 in Lindburg DG, ed. The Macaques: Studies in Ecology, Behavior, and Evolution. Van Nostrand Reinhold Co.

Dhawale AK, Kumar MA, Sinha A. 2020. Changing ecologies, shifting behaviours: Behavioural responses of a rainforest primate, the lion-tailed macaque *Macaca silenus*, to a matrix of anthropogenic habitats in southern India. PLOS One 15: 1–19.

Diamond JM. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7: 129–146.

Diamond JM. 1984. "Normal" extinctions of isolated populations. Pages 191–246 in Nitecki MN, ed. Extinctions. The University of Chicago Press.

Duncan JH. 2006. The changing concept of animal sentience. Applied Animal Behaviour Science 100: 11–19.

Edwards KL, Shultz S, Pilgrim M, Walker SL. 2015. Irregular ovarian activity, body condition and behavioural differences are associated with reproductive success in female eastern black rhinoceros (*Diceros bicornis michaeli*). General and Comparative Endocrinology 214: 186–194.

Eisenberg JF, Kleiman DG. 1977. The usefulness of behaviour studies in developing captive breeding programmes for mammals. International Zoo Yearbook 17: 81–89.

Eppley TM, et al. 2022. Factors influencing terrestriality in primates of the Americas and Madagascar. The Proceedings of the National Academy of Sciences 42: e2121105119.

Erwin J, Maple TL, Mitchell G, eds. 1979. Captivity and Behavior. Primate Behavior and Development Series. Van Nostrand Rheinhold.

Estrada A, et al. 2017. Impending extinction crisis of the world's primates: Why primates matter. Science Advances 3: e1600946.

Fa JE, Funk SM, O'Connell D. 2011. Zoo Conservation Biology. Cambridge University Press.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487–515.

Fahrig L, Merriam G. 1994. Conservation of fragmented populations. Conservation Biology 8:

50–59.

Fernandez EJ, Martin AL. 2021. Animal training, environment enrichment, and animal welfare: A history of behavior analysis in zoos. Journal of Zoological and Botanical Gardens 2: 531–543.

Fischer J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: A synthesis. Global Ecology and Biogeography 16: 265–280.

Flather CH, Hayward GD, Beissinger SR, Stephens PA. 2011a. Minimum viable populations: Is there a 'magic number' for conservation practitioners? Trends in Ecology & Evolution 26: 307–316.

Flather CH, Hayward GD, Beissinger SR, Stephens PA. 2011b. A general target for MVPs: Unsupported and unnecessary. Trends in Ecology and Evolution 26: 620–622.

Fooden J. 1975. Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). Fieldiana Zoology 67: 1–169.

Fooden J. 1980. Classification and distribution of living macaques. Pages 1–9 in Lindburg DG, ed. The Macaques: Studies in Ecology, Behavior, and Evolution. Van Nostrand Reinhold Co.

Forthman DL, Ogden JJ. 1992. The role of applied behavior analysis in zoo management: Today and tomorrow. Journal of Applied Behavior Analysis 25: 647–652.

Forthman-Quick DL. 1984. An integrative approach to environmental engineering in zoos. Zoo Biology 3: 65–77.

Frankel OH, Soulé ME. 1981. Conservation and Evolution. Cambridge University Press.

Frankham R. 1995. Conservation genetics. Annual Review of Genetics 29: 305–327.

Frankham R. 1999. Quantitative genetics in conservation biology. Genetics Research 74: 237–244.

Frankham R, Ballou JD, Briscoe DA. 2002. Introduction to Conservation Genetics. Cambridge University Press.

Frankham R, Ballou JD, Briscoe DA. 2010. Introduction to Conservation Genetics. 2nd ed. Cambridge University Press.

Frankham R, Bradshaw CJ, Brook BW. 2014. Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. Biological Conservation 170: 56–63.

Franklin IR. 1980. Evolutionary change in small populations. Pages 135–150 in Soulé ME, Wilcox BA, eds. Conservation Biology: An Evolutionary–Ecological Perspective. Sinauer Associates.

Franklin JF. 1993. Preserving biodiversity: Species, ecosystems, or landscapes? Ecological Applications 3: 202–205.

Gibbons JW, et al. 2000. The global decline of reptiles, déjà vu amphibians: Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. BioScience 50: 653–666.

Gilbert T, Soorae PS. 2017. Editorial: The role of zoos and aquariums in reintroductions and other conservation translocations. International Zoo Yearbook 51: 9–14.

Gilpin ME, Diamond JM. 1976. Calculation of immigration and extinction curves from the species-area-distance relation. Proceedings of National Academy of Sciences 73: 4130–4134.

Gilpin ME, Diamond JM. 1980. Subdivision of nature reserves and the maintenance of species diversity. Nature 285: 567–568.

Gilpin ME, Soulé ME. 1986. Minimum viable populations: Processes of species extinction. Pages 19–34 in Soulé ME, ed. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates.

Glatston A, Leus K. 2005. Global Captive Breeding Masterplan for the Red or Lesser Panda *Ailurus fulgens fulgens* and *Ailurus fulgens styani*. Royal Rotterdam Zoological and Botanical Gardens.

Gledhill LG. 1987. Lion-tailed Macaque International Studbook. Woodland Park Zoological Gardens.

Gledhill LG. 1990. Species coordinator's report. Lion-Tales 7(Summer): 1.

Gosling LM. 2003. Adaptive behavior and population viability. Pages 13–30 in Festa-Bianchet M, Apollonio M, eds. Animal Behavior and Wildlife Conservation. Island Press.

Goss-Custard JD, Stillman RA. 2008. Individual-based models and the management of shorebird populations. Natural Resource Modeling 21: 3–71.

Griffith B, Scott JM, Carpenter JW, Reed C. 1989. Translocation as a species conservation tool: Status and strategy. Science 245: 477–480.

Grimm V, Railsback SF. 2005. Individual-based modeling and ecology. Princeton University Press.

Hancocks D. 1980. Bringing nature into the zoo: Inexpensive solutions for zoo environments.

International Journal of Studies of Animal Problems 1: 170–177.

Harlow HF. 1958. The nature of love. American Psychologist 13: 673–685.

Harlow HF, Harlow MK. 1962. Social deprivation in monkeys. Scientific American 207: 136–150.

Harvey NC, Lindburg DG. 2001. A long-term decline in swelling of the sexual skin in captive lion-tailed macaques. Primate Report 59: 43–49.

Hediger H. 1942. Wildtiere in Gefangenschaft: Ein Grundriss der Tiergartenbiologie. Benno Schwabe and Co., Verlag.

Hediger H. 1950. Wild Animals in Captivity: An Outline of the Biology of Zoological Gardens.

Butterworths Scientific Publications.

Hediger H. 1969. Man and Animal in the Zoo: Zoo Biology. Vevers G, Reade W (Trans.).

Delacorte Press.

Hediger H. 1982. Zoo Biology: Retrospect and prospect. Zoo Biology 1: 85–88.

Heistermann M, Uhrigshardt J, Husung A, Kaumanns W, Hodges JK. 2001. Measurement of faecal steroid metabolites in the lion-tailed macaque (*Macaca silenus*): A non-invasive tool for assessing female ovarian function. Primate Report 59: 27–42.

Heltne PG, ed. 1985. The Lion-tailed Macaque: Status and Conservation. Monographs in Primatology, vol. 7. Alan R. Liss.

Hermes R, Hildebrandt TB, Göritz F. 2004. Reproductive problems directly attributable to long-term captivity – asymmetric reproductive aging. Animal Reproduction Science 82–83: 49–60.

Hermes R et al. 2006. The effect of long non-reproductive periods on the genital health in captive female white rhinoceroses (*Ceratotherium simum simum, C. s. cottoni*). Theriogenology 65: 1492–1515.

Hildebrandt TB., Göritz F, Hermes R, Reid C, Dehnhard M, Brown JL. 2006. Aspects of the reproductive biology and breeding management of Asian and African elephants *Elephas maximus* and *Loxodonta africana*. International Zoo Yearbook 40: 20–40.

Hodges JK, Kaumanns W, Gansloßer U. 1995. Zoobiology: A scientific basis for animal management and conservation. Pages 7–9 in Gansloßer U, Hodges JK, Kaumanns W, eds. Research and Captive Propagation. Filander Verlag.

Hofer H, East ML. 2003. Behavioural processes and costs of co-existence in female spotted hyenas: A life history perspective. Evolutionary Ecology 17: 315–331.

Hoffmann M, et al. 2010. The impact of conservation on the status of the world's vertebrates. Science 330: 1503–1509.

Huston M, DeAngelis D, Post W. 1988. New computer models unify ecological theory. BioScience 38: 682–691.

Hussain S, Ram MS, Kumar A, Shivaji S, Umapathy G. 2013. Human presence increases parasitic load in endangered lion-tailed macaques (*Macaca silenus*) in its fragmented rainforest habitats in southern India. PlOS ONE 8: e63685.

Hutchins M, Hancocks D, Calip T. 1978a. Behavioral engineering in the zoo: A critique. International Zoo News 25(Part I): 18–23.

Hutchins M, Hancocks D, Calip T. 1978b. Behavioral engineering in the zoo: A critique. International Zoo News 25(Part II): 18–23.

Hutchins M, Hancocks D, Calip T. 1979. Behavioral engineering in the zoo: A critique. International Zoo News 26(Part III): 20–27.

Hutchins M, Hancocks D, Crockett C. 1984. Natural solutions to the behavioral problems of captive animals. Der Zoologische Garten 54: 28–42.

Hutchins M, Wiese RJ, Smith B. 2019. Research in zoos and aquariums: Purpose, justification, utility, and welfare. Pages 1–42 in Kaufman AB, Bashaw MJ, Maple TL, eds. Scientific Foundations of Zoos and Aquariums: Their Role in Conservation and Research. Cambridge University Press.

Jeganathan P, Mudappa D, Raman TRS, Kumar MA. 2018a. Understanding perceptions of people towards lion-tailed macaques in a fragmented landscape of the Anamalai Hills, Western Ghats, India. Primate Conservation 32: 205–215.

Jeganathan P, Mudappa D, Kumar MA, Raman TRS. 2018b. Seasonal variation in wildlife roadkills in plantations and tropical rainforest in the Anamalai Hills, Western Ghats, India. Current Science 114: 619–626.

Jeyraj T. 2003. A Study of Male Behavior in Lion-tailed Macaques (*Macaca silenus*) with Special Reference to Male-Male Interactions. Master's thesis. University of Mysore, Mysore, India.

Johns AD. 1992. Vertebrate responses to selective logging: Implications for the design of logging systems. Philosophical Transactions of the Royal Society London B 335: 437–442.

Kaiser H. 1979. The dynamics of populations as result of the properties of individual animals.

Fortschritte der Zoologie 25: 109–136.

Kaumanns W, Rohrhuber B. 1995. Captive propagation in lion-tailed macaques: The status of the European population and research implications. Pages 296–309 in Gansloßer U, Hodges JK, and Kaumanns W, eds. Research and Captive Propagation. Filander Verlag.

Kaumanns W, Singh M. 2015. Towards more individual-based and fitness-oriented captive mammal population management. Current Science 109: 1121–1129.

Kaumanns W, Schwitzer C, Schmidt P, Knogge C. 2001. The European lion-tailed macaque population: An overview. Primate Report 59: 65–76.

Kaumanns W, Krebs E, Singh M. 2006. An endangered species in captivity: Husbandry and management of the lion-tailed macaque (*Macaca silenus*). MyScience 1: 43–71.

Kaumanns W, Singh M, Krebs E, Schwitzer C. 2008. Primate populations in zoos: A case of fragmentation. Primate Report 76: 41–54.

Kaumanns W, Singh M, Sliwa A. 2013. Captive propagation of threatened primates – the example of the lion-tailed macaque *Macaca silenus*. Journal of Threatened Taxa 5: 4825–4839.

Kierulff MCM, Ruiz-Miranda CR, Oliveira PP, Beck BB, Martins A, Dietz JM, Rambaldi DM, Baker AJ. 2012. The Golden lion tamarin *Leontopithecus rosalia*: A conservation success story. International Zoo Yearbook 46: 36–45.

Kleiman DG. 1992. Behavior research in zoos: Past, present, and future. Zoo Biology 11: 301–312.

Kleiman DG. 1996a. Preface. Pages xv–xvi in Kleiman DG, Allen ME, Thompson KV, Lumpkin S, Harris H, eds. Wild Mammals in Captivity: Principles and Techniques for Zoo Management. 1st ed. The University of Chicago Press.

Kleiman DG. 1996b. Reproduction, introduction. Pages 377–378 in Kleiman DG, Allen ME, Thompson KV, Lumpkin S, Harris H, eds. Wild Mammals in Captivity: Principles and Techniques for Zoo Management. 1st ed. The University of Chicago Press.

Kleiman DG, Mallinson JJC. 1998. Recovery and management committees for lion tamarins: Partnerships in conservation planning and implementation. Conservation Biology 12: 27–38.

Kleiman DG, Thompson K, Kirk Baer C, eds. 2010. Wild Mammals in Captivity: Principles and Techniques for Zoo Management. 2nd ed. The University of Chicago Press.

Knowles J. 2003. Zoos and a century of change. International Zoo Yearbook 38: 28–34.

Kreger MD, Hutchins M. 2010. Ethics of keeping mammals in zoos and aquariums. Pages 3–10 in Kleiman DG, Thompson KV, Kirk Baer C, eds. Wild Mammals in Captivity: Principles and Techniques for Zoo Management. 2nd ed. The University of Chicago Press.

Krishna BA, Singh M, Singh M. 2006. Population dynamics of a group of lion-tailed macaques (*Macaca silenus*) inhabiting a rainforest fragment in the Western Ghats, India. Folia Primatologica 77: 377−386.

Krishnadas M, Chandrasekhara K, Kumar A. 2011. The response of the frugivorous lion-tailed macaque (*Macaca silenus*) to a period of fruit scarcity. American Journal of Primatology 73: 1250–1260.

Krishnakumar N, Manimozhi A. 2000. What ails captive breeding programmes in India – lion-tailed macaque (ltm) – A case study. Zoos' Print Journal 15: 421–422.

Krishnamani R, Kumar A. 2018. Why are lion-tailed macaques rare? Pages 285–294 in Sivaperuman C, Venkataraman K, eds. Indian Hotspots: Vertebrate Faunal Diversity, Conservation and Management, vol. 1. Springer.

Kumar A. 1985. Patterns of extinction in India, Sri Lanka and elsewhere in southeast Asia: Implications for lion-tailed macaque wildlife management and the Indian conservation system. Pages 65–90 in Heltne PG, ed. The Lion-tailed Macaque: Status and Conservation. Monographs in Primatology, vol. 7. Alan R. Liss.

Kumar A. 1987. The ecology and population dynamics of the Lion-tailed Macaque (*Macaca silenus*) in south India. PhD dissertation. University of Cambridge, Cambridge, United Kingdom.

Kumar A. 1995. Birth rate and survival in relation to group size in the lion-tailed macaque, *Macaca silenus*. Primates 36: 1–9.

Kumar A. 2000. Sexual harassment among female lion-tailed macaques (*Macaca silenus*) in the wild. Journal of Bombay Natural History Society 97: 42–51.

Kumar A, Kurup GU. 1985a. Inter-troop interactions in the lion-tailed macaque *Macaca silenus*. Pages 91–107 in Heltne PG, ed. The Lion-tailed Macaque: Status and Conservation. Monographs in Primatology, vol. 7. Alan R. Liss Inc.

Kumar A, Kurup GU. 1985b. Sexual behaviour of the Lion-tailed Macaque (*Macaca silenus*). Pages 109–130 in Heltne PG, ed. The Lion-tailed Macaque: Status and Conservation. Monographs in Primatology, vol. 7. Alan R. Liss Inc.

Kumar A, Umapathy G, Prabhakar A. 1995a. A study on the management and conservation of the small mammals in fragmented rain forests of Western Ghats, south India: A preliminary report. Primate Conservation 16: 53–58.

Kumar A, Molur S, Walker S. 1995b. Lion-tailed Macaque Population and Habitat Viability Assessment Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota.

Kumar MA, Singh M, Kumara HN, Sharma AK, Bertsch C. 2001. Male migration in lion-tailed macaques. Primate Report 59: 5–18.

Kumar MA, Vijayakrishnan S, Singh M. 2018. Whose habitat is it anyway? Role of natural and anthropogenic habitats in conservation of charismatic species. Tropical Conservation Science 11: 1–5.

Kumara HN, Singh M. 2004a. The influence of differing hunting practices on the relative abundance of mammals in two rainforest areas of the Western Ghats, India. Oryx 38: 321–327.

Kumara HN, Singh M. 2004b. Distribution and abundance of primates in rain forests of the Western Ghats, Karnataka, India and the conservation of *Macaca silenus*. International Journal of Primatology 25: 1001–1018.

Kumara HN, Sinha A. 2009. Decline of the endangered lion-tailed macaque in the Western Ghats, India. Oryx 43: 292–298.

Kumara HN, Pritham NS, Santhosh K, Raj VVM, Sinha A. 2011. Decline of suitable habitats and conservation of the endangered lion-tailed macaque: Land-cover change at a proposed protected area in Sirsi Honnavara, Western Ghats, India. Current Science 10: 434–439.

Kumara HN, Sasi R, Suganthasakthivel R, Singh M, Sushma HS, Ramachandran KK, Kaumanns W. 2014. Distribution, demography, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anamalai Hills Landscape, Western Ghats, India. International Journal of Primatology 35: 976–989.

Kurup GU, Kumar A. 1993. Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). International Journal of Primatology 14: 27–39.

Lacy RC. 2013. Achieving true sustainability of zoo populations. Zoo Biology 32: 19–26.

Lasley BL, Czekala NM, Lindburg DG. 1985. Urinary estrogen profile in the lion-tailed macaque. Pages 149–159 in Heltne PG, ed. The Lion-tailed Macaque: Status and Conservation. Monographs in Primatology, vol. 7. Alan R. Liss.

Lees CM, Wilcken J. 2009. Sustaining the ark: The challenges faced by zoos in maintaining viable populations. International Zoo Yearbook 43: 6–18.

Leus K, Lackey LB, van Lint W, de Man D, Riewald S, Veldkam A, Wijmans J. 2011a. Sustainability of European Association of Zoos and Aquaria bird and mammal populations. WAZA Magazine 12: 11–14.

Leus K, Traylor-Holzer K, Lacy RC. 2011b. Genetic and demographic population management in zoos and aquariums: Recent developments, future challenges and opportunities for scientific research. International Zoo Yearbook 45: 213–225.

Levins R. 1968. Evolution in Changing Environments. Princeton University Press.

Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237–240.

Levins R. 1970. Extinction. Pages 77–107 in Gerstenhaber M, ed. Some Mathematical Problems in Biology, 2nd vol. American Mathematical Society.

Lindburg DG. 1980. Status and captive reproduction of the lion-tailed macaque *Macaca silenus*. International Zoo Yearbook 20: 60–64.

Lindburg DG. 1990. Proceptive calling by the female lion-tailed macaque. Zoo Biology Supplement 9: 437–446

Lindburg DG. 1993. Macaques may have a bleak future in North American zoos. Zoo Biology 12: 407–409

Lindburg DG. 2001. A century of involvement with lion-tailed macaques in North America. Primate Report 58: 51–64.

Lindburg DG, Fitch-Snyder H. 1994. Use of behavior to evaluate reproductive problems in captive mammals. Zoo Biology 13: 433–445.

Lindburg DG, Forney KA. 1992. Long-term studies of captive lion-tailed macaques. Primate Report 32: 133–142.

Lindburg DG, Shideler S, Fitch-Snyder H. 1985. Sexual behavior in relation to the time of ovulation in the lion-tailed macaque. Pages 131–148 in Heltne PG, ed. The Lion-tailed Macaque: Status and Conservation. Monographs in Primatology, vol. 7. Alan R. Liss.

Lindburg DG, Lyles AM, Czekala NM. 1989. Status and reproductive potential of lion-tailed macaques in captivity. Zoo Biology Supplement 1: 5–16.

Lomnicki A. 1978. Individual differences between animals and the natural regulation of their numbers. Journal of Animal Ecology 47: 461–475.

Lomnicki A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos 35: 185–193.

Lomnicki A. 1999. Individual-based models and the individual-based approach to population ecology. Ecological Modelling 115: 191–198.

Long S, Dorsey C, Boyle P. 2011. Status of association of zoos and aquariums cooperatively managed programs. WAZA Magazine 12: 15–18.

Lott DF. 1991. Intraspecific Variation in the Social System of Wild Vertebrates. Cambridge University Press.

Ludwig C, Dehnhard M, Pribbenow S, Silinski-Mehr S, Hofer H, Wachter B. 2019. Asymmetric reproductive aging in cheetah (*Acinonyx jubatus*) females in European zoos. Journal of Zoo and Aquarium Research 7: 87–93.

Maple TL. 1979. Great apes in captivity: The good, the bad and the ugly. Pages 239–272 in Erwin J, Maple T, Mitchell G, eds. Captivity and Behavior: Primates in Breeding Colonies, Laboratories and Zoos. Van Nostrand Reinhold.

Maple TL. 2007. Toward a science of welfare for animals in the zoo. Journal of Applied Animal Welfare Science 10: 63–70

Maple TL, Perdue BM. 2013. Zoo Animal Welfare. Springer.

Markowitz H. 1979. Environmental enrichment and behavioral engineering for captive primates. Pages 217–238 in Erwin J, Maple T, Mitchell G, eds. Captivity and Behavior: Primates in Breeding Colonies, Laboratories and Zoos. Van Nostrand Reinhold.

Markowitz H. 1982. Behavioral Enrichment in the Zoo. Van Nostrand Reinhold.

Markowitz H, Aday C. 1998. Power for captive animals: Contingencies and nature. Pages 47–58 in Shepherdson DJ, Mellen JD, Hutchins M, eds. Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press.

Marsh LK. 2003. Primates in Fragments: Ecology and Conservation. Kluwer Academic/Plenum Publishers.

Marsh LK, Chapman C. 2013. Primates in Fragments: Complexity and Resilience. Springer.

Martin MS, Shepherdson DJ. 2012. Role of familiarity and preference in reproductive success in *ex situ* breeding programs. Conservation Biology 26: 649–656.

Mason G, Burn CC, Dallaire JA, Kroshko J, McDonald Kinkaid H, Jeschke JM. 2013. Plastic animals in cages: Behavioural flexibility and responses to captivity. Animal Behaviour 85: 1113–1126.

May R. 2010. Ecological science and tomorrow's world. Philosophical Transactions of the Royal Society B 365: 41–47.

McPhee ME & Carlstead K. 2010. The importance of maintaining natural behaviors in captive mammals. Pages 303–313 in Kleiman DG, Thompson KV, Kirk Baer C, eds. Wild Mammals in Captivity: Principles and Techniques for Zoo Management. 2nd ed. The University of Chicago Press.

Mellen J, MacPhee MS. 2001. Philosophy of environmental enrichment: Past, present, and future. Zoo Biology 20: 211–226.

Mellen J, Shepherdson DJ. 1997. Environmental enrichment for felids: An integrated approach. International Zoo Yearbook 35: 191–197.

Melnick DJ. 1990. Report on the third lion-tail macaque symposium. Lion-Tales 7(Summer): 2–4.

Menon S, Bawa KS. 1997. Applications of geographic information systems, remote-sensing, and a landscape ecology approach to biodiversity conservation in the Western Ghats. Current Science 73: 134–145.

Molur S, Brandon-Jones D, Dittus W, Eudey A, Kumar A, Singh M, Feeroz MM, Chalise M, Priya P, Walker S. 2003. Status of South Asian Primates: Conservation Assessment and Management Plan (C.A.M.P.) Workshop Report. Zoo Outreach Organisation, CBSG-South Asia, Coimbatore India.

Montgomery ME, Ballou JD, Nurthen RK, England PR, Briscoe DA, Frankham R. 1997. Minimizing kinship in captive breeding programs. Zoo Biology 16: 377–389.

Morgan KN, Tromborg CT. 2007. Sources of stress in captivity. Applied Animal Behaviour Science 102: 262–302.

Myers N. 1979. The Sinking Ark: A New Look at the Problem of Disappearing Species. Pergamon Press.

Ness T. 2013. North American Studbook for Lion-tailed Macaques (*Macaca silenus*). Minnesota Zoological Gardens.

Novak MA, Meyer JS, Lutz C, Tiefenbacher S. 2006. Deprived environments: Developmental insights from primatology. Pages 153–189 in Mason G, Rushen J eds. Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare: 2nd ed. Cromwell Press.

Penfold LM, Powell D, Traylor-Holzer K, Asa CS. 2014. "Use it or lose it": Characterization, implications, and mitigation of female infertility in captive wildlife. Zoo Biology 33: 20–28.

Powell DM, Watters JV. 2017. The evolution of the animal welfare movement in U.S. zoos and aquariums. Der Zoologische Garten 86: 219–234.

Powell DM, Dorsey CL, Faust LJ. 2019. Advancing the science behind animal program sustainability: An overview of the special issue. Zoo Biology 38: 5–11.

Prado-Oviedo NA, Bonaparte-Saller MK, Malloy EJ, Meehan CL, Mench JA, Carlstead K, Brown JL. 2016. Evaluation of demographics and social life events of Asian (*Elephas maximus*) and African elephants (*Loxodonta africana*) in North American zoos. PLOS ONE 11: e0154750.

Princée FPG. 2016. Exploring Studbooks for Wildlife Management and Conservation. Topics in Biodiversity and Conservation, vol. 17. Springer Nature.

Princée FPG, Glatston AR. 2016. Influence of climate on the survivorship of neonatal red pandas in captivity. Zoo Biology 35: 104–110.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society of London B 267: 1947–1952.

Putnam AS, Ferrie GM, Ivy JA. 2022. *Ex situ* breeding programs benefit from science-based cooperative management. Zoo Biology (May).

Quammen D. 2004. The Song of Dodo: Island Biogeography in an Age of Extinctions. Scribner.

Ram MS, Marne M, Gaur A, Kumara HN, Singh M, Kumar A, Umapathy G. 2015. Pre-historic and recent vicariance events shape genetic structure and diversity in endangered lion-tailed macaque in the Western Ghats: Implications for conservation. PLOS ONE 10: e0142597.

Ramachandran KK, Joseph GK. 2000. Habitat utilization of lion-tailed macaque (*Macaca silenus*) in Silent Valley National Park, Kerala, India. Primate Report 58: 17–25.

Rees PA. 2003. Asian elephants in zoos face global extinction: Should zoos accept the inevitable? Oryx 37: 20–22.

Rees PA. 2009. The sizes of elephant groups in zoos: Implications for elephant welfare. Journal of Applied Animal Welfare Science 12: 44–60.

Ricklefs RE. 1991. Structures and transformations of life histories. Functional Ecology 5: 174–183.

Ricklefs RE, Wikelski M. 2002. The physiology/life-history nexus. Trends in Ecology and Evolution 17: 462–468.

Rockwood LL. 2006. Introduction to Population Ecology. Blackwell Publishing.

Rode KD, Chapman CA, McDowell LR, Stickler C. 2006. Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). Biotropica 38: 625–634.

Saunders SP, Harris T, Traylor-Holzer K, Beck KG. 2014. Factors influencing breeding success, ovarian cyclicity, and cub survival in zoo-managed tigers (*Panthera tigris*). Animal Reproduction Science 144: 38– 47.

Schmidt H, Kappelhof J. 2019. Review of the management of the Asian elephant (*Elephas maximus*) EEP: Current challenges and future solutions International Zoo Yearbook 53: 31–44.

Schonewald-Cox C, Chambers S, MacBryde B, Thomas L, eds. 1983. Genetics and conservation: A reference manual for managing wild animal and plant populations. Benjamin/Cummings.

Schreiber A, Kolter L, Kaumanns W. 1993. Conserving patterns of genetic diversity in endangered mammals by captive breeding. Acta Theriologica Supplement 38: 71–88.

Schulte BA. 2000. Social structure and helping behaviour in captive elephants. Zoo Biology 19: 447–459.

Schulte-Hostedde AI, Mastromonaco GF. 2015. Integrating evolution in the management of captive zoo populations. Evolutionary Applications 8: 413–422.

Schwibbe M, Singh M, Kaumanns W, Knogge C, eds. 2000. Proceedings of the Fifth International Symposium on Lion-tailed Macaque, Mysore, India, Part 1. Primate Report 58. German Primate Center.

Schwibbe M, Singh M, Kaumanns W, Knogge C, eds. 2001. Proceedings of the Fifth International Symposium on Lion-tailed Macaque, Mysore, India, Part 2. Primate Report 59. German Primate Center.

Scobie P, Bingaman Lackey L. 2012. SPARKS: Single Population Analysis & Records Keeping System. Version 1.66. International Species Information System (renamed to Species360).

Seal US, Thorne ET, Bogan MA, Anderson SH. 1989. Conservation Biology and the Black-footed Ferret. Yale University Press.

Seidensticker J, Forthman DL. 1998. Evolution, ecology, and enrichment: Basic considerations for wild animals in zoos. Pages 15–29 in Shepherdson D, Mellen J, Hutchins M, eds. Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press.

Shaffer ML. 1978. Determining Minimum Viable Population Sizes: A Case Study of the Grizzly Bear (*Ursus arctos L.*) PhD dissertation. Duke University, Durham, North

Carolina, USA.

Shaffer ML. 1981. Minimum population sizes for species conservation. BioScience 31: 131–134.

Sharma AK. 2002. A Study of Reproductive Behaviour of Lion-tailed Macaque (*Macaca silenus*) in the Rainforests of Western Ghats. PhD dissertation. University of Mysore, Mysore, India.

Sharma A, Singh M, Kaumanns W, Krebs E, Singh M, Kumar MA, Kumara HN. 2006. Birth patterns in wild and captive lion-tailed macaques (*Macaca silenus*). International Journal of Primatology 27: 1429–1439.

Sheldon BC, Kruuk LEB, Alberts SC. 2022. The expanding value of long-term studies of individuals in the wild. Nature Ecology & Evolution 6: 1799–1801

Shepherdson DJ. 1998. Tracing the path of environmental enrichment in zoos. Pages 1–12 in Shepherdson DJ, Mellen JD, Hutchins M, eds. Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press.

Shepherdson DJ, Mellen JD, Hutchins M. 1998. Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press.

Shideler SE, Czekala NM, Kasman LH, Lindburg DG, Lasley BL. 1983. Monitoring ovulation and implantation in the lion-tailed macaque (*Macaca silenus*) through urinary estrone con jugate evaluations. Biology of Reproduction 29: 905–911.

Sih A, Ferrari MCO, Harris DJ. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4: 367–387.

Singh M. 2019. Management of forest-dwelling and urban species: Case studies of the lion-tailed macaque (*Macaca silenus*) and the bonnet macaque (*M. radiata*). International Journal of Primatology 40: 613–629.

Singh M, Kaumanns W. 2005. Behavioural studies: A necessity for wildlife management. Current Science 89: 1230–1236.

Singh M, Singh M, Kumara HN, Kumar MA, D'Souza L. 1997. Inter- and intra-specific associations of non-human primates in Anaimalai Hills, south India. Mammalia 61: 17–28.

Singh M, Kumara HN, Ananda Kumar M, Sharma AK, De Falco K. 2000. Status and conservation of lion-tailed macaque and other arboreal mammals in tropical rainforests of Sringeri Forest Range, Western Ghats, Karnataka, India. Primate Report 58: 5–16.

Singh M, Kumara HN, Kumar MA, Sharma AK. 2001. Behavioural responses of lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rainforest fragment in the Western Ghats, India. Folia Primatologica 72: 278–291.

Singh M, Singh M, Kumar MA, Kumara HN, Sharma AK, Kaumanns W. 2002. Distribution, population structure, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anaimalai Hills, Western Ghats, India. American Journal of Primatology 57: 91–102.

Singh M, Sharma AK, Krebs E, Kaumanns W. 2006a. Reproductive biology of lion-tailed macaque (*Macaca silenus*): An important key to the conservation of an endangered species. Current Science 90: 804–811.

Singh M, Krishna BA, Singh M. 2006b. Dominance hierarchy and social grooming in female lion-tailed macaques (*Macaca silenus*) in the Western Ghats, India. Journal of Biosciences

31: 369–377.

Singh M, Kaumanns W, Singh M, Sushma HS, Molur S. 2009. The lion-tailed macaque *Macaca silenus* (Primates : Cercopithecidae): Conservation history and status of a flagship species of the tropical rainforests of the Western Ghats, India. Journal of Threatened Taxa 1: 151–157.

Singh M, Jeyaraj T, Prashanth U, Kaumanns W. 2010. Male-male relationships in lion-tailed macaques (*Macaca silenus*) and bonnet macaques (*Macaca radiata*). International Journal of Primatology 32: 166–176.

Singh M, Kumar A, Kumara HN. 2020. *Macaca silenus*. The IUCN Red List of Threatened Species 2020: e.T12559A17951402. (16 July 2021; *www.iucnredlist.org*)

Skinner BF. 1938. The Behavior of Organisms: An Experimental Analysis. Appleton-Century-Crofts, Inc.

Skinner BF. 1948. “Superstition” in the pigeon. Journal of Experimental Psychology 38: 168–172.

Skinner BF. 1953. Science and Human Behaviour. Free Press.

Skinner BF. 1974. About Behaviorism. Alfred A. Knopf Inc.

Skorupa JP. 1986. Responses of rainforest primates to selective logging in Kibale Forest, Uganda: A summary report. Pages 57–70 in Benirschke K, ed. Primates: The Road to Self-Sustaining Populations. Springer-Verlag.

Sliwa A, Begum N. 2019. International Studbook 2018 for the Lion-tailed Macaque *Macaca silenus* Linnaeus, 1758, vol. 9. Edition 2018. Zoologischer Garten Köln.

Snyder NFR, Snyder H. 2000. The California Condor: A Saga of Natural History and Conservation. Princeton University Press.

Sorci G, Lesobre L, Vuarin P, Levêque G, Saint Jalme M, Lacroix F, Hingrat Y. 2021. Enforced monoandry over generations induces a reduction of female investment into reproduction in a promiscuous bird. Evolutionary Applications 14: 2773–2783.

Soulé ME. 1985. What is conservation biology: A new synthetic discipline addresses the dynamics and problems of perturbed species, communities and ecosystems. BioScience 35: 727–734.

Soulé ME, ed. 1986. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates.

Soulé ME, Wilcox BA, eds. 1980. Conservation Biology: An Evolutionary Ecological Perspective. Sinauer.

Soulé M, Gilpin M, Conway W, Foose T. 1986. The millenium ark: How long a voyage, how many staterooms, how many passengers? Zoo Biology 5: 101–113.

Stanley Price MR. 1989. Animal Re-introductions: The Arabian Oryx in Oman. Cambridge University Press.

Stanley Price MR, Fa JE. 2007. Reintroduction from zoos: Guiding light or shooting star? Pages 155–177 in Zimmerman A, Hatchwell M, Dickie L, West C, eds. Zoos in the 21st Century: Catalysts for Conservation? Cambridge University Press.

Stearns SC. 1976. Life-history tactics: A review of the ideas. The Quarterly Review of Biology 51: 3–47.

Stearns SC. 1977. The evolution of life history traits : A critique of the theory and a review of the data. Annual Review of Ecology and Systematics 8: 145–171.

Stearns SC. 1992. The Evolution of Life Histories. Oxford University Press.

Stearns SC. 2000. Life history evolution : Successes, limitations, and prospects. Naturwissenschaften 87: 476–486.

Stephens PA, Sutherland WJ, Freckleton RP. 1999. What is the Allee effect? Oikos 87: 185–190.

Stevens PMC, McAlister E. 2003. Ethics in zoos. International Zoo Yearbook 38: 94–101.

Stillman RA, Railsback SF, Giske J, Berger U, Grimm V. 2015. Making predictions in a changing world: The benefits of individual-based ecology. BioScience 65: 140–150.

Struhsaker TT. 1997. Ecology of an African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation. University Press of Florida.

Sushma HS, Singh M. 2006. Resource partitioning and interspecific interaction among sympatric rain forest arboreal mammals of the Western Ghats, India. Behavioral Ecology 17: 479–490.

Sushma HS, Mann R, Kumara HN, Udhayan A. 2014. Population status of the endangered lion-tailed macaque *Macaca silenus* in Kalakad-Mundanthurai Tiger Reserve, Western Ghats, India. Primate Conservation 28: 171–178.

Sutherland WJ, Gosling L. 2000. Advances in the study of behaviour and their role in conservation. Pages 3–9 in Gosling L, Sutherland WJ, eds. Behaviour and Conservation. Cambridge University Press.

Swaisgood RR, Schulte BA. 2010. Applying knowledge of mammalian social organization, mating systems and communication to management. Pages 329–343 in Kleiman DG, Thompson KV, Baer CK, eds. Wild Mammals in Captivity: Principles and Techniques for Zoo Management. 2nd ed. The University of Chicago Press.

Swaisgood RR, Dickman DM, White AM. 2006. A captive population in crisis : Testing hypotheses for reproductive failure in captive-born southern white rhinoceros females. Biological Conservation 129: 468–476.

Thierry B, Singh M, Kaumanns W, eds. 2004. Macaque Societies: A Model for the Study of Social Organization. Cambridge University Press.

Traill LW, Brook BW, Frankham RR, Bradshaw CJA. 2010. Pragmatic population viability targets in a rapidly changing world. Biological Conservation 143: 28–34.

Turchin P. 2003. Complex Population Dynamics: A Theoretical/Empirical Synthesis. Princeton University Press.

Umapathy G. 1998. Impact of Habitat Fragmentation on the Arboreal Mammals in the Wet Evergreen Forests of Anamalai Hills in the Western Ghats, South India. PhD dissertation. Bharathiar University, Coimbatore, India.

Umapathy G, Kumar A. 2000. The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Anamalai Hills, south India. Primates 41: 119–126.

Umapathy G, Kumar A. 2003. Impacts of forest fragmentation on lion-tailed macaque and Nilgiri langur in Western Ghats, south India. Pages 163–189 in Marsh LK, ed. Primates in Fragments: Ecology and Conservation. Kluwer Academic/Plenum Press.

Umapathy G, Hussain S, Shivaji S. 2011. Impact of habitat fragmentation on the demography of lion-tailed macaque (*Macaca silenus*) populations in the rainforests of Anamalai Hills, Western Ghats, India. International Journal of Primatology 32: 889–900.

Uphouse L. 1980. Reevaluation of mechanisms that mediate brain differences between enriched and impoverished animals. Psychological Bulletin 88: 215–232.

von Uexküll J. 1957. A stroll through the world of animals and men: A picture book of invisible worlds. Pages 5–80 in Schiller CH, ed. (Trans.), Instinctive Behavior. International Universities Press.

Wachter B, Thalwitzer S, Hofer H, Lonzer J, Hildebrandt TB, Hermes R. 2011. Reproductive history and absence of predators are important determinants of reproductive fitness: The cheetah controversy revisited. Conservation Letters 4: 47–54.

Walters CJ, Hilborn R. 1978. Ecological optimization and adaptive management. Annual Review of Ecology, Evolution, and Systematics 9: 157–188.

Watson JB. 1928. The Ways of Behaviorism. Harper & Brothers.

Watters JV, Lema SC, Nevitt GA. 2003. Phenotype management: A new approach to habitat restoration. Biological Conservation 112: 435–445.

Watters JV, Bremner-Harrison S, Powell DM. 2017. Phenotype management: An inclusive framework for supporting individual's contributions to conservation populations. Pages 277–294 in Vonk J, Weiss A, Kuczaj SA, eds. Personality in Nonhuman Animals. Springer.

[WAZA] World Association of Zoos and Aquariums. (29 December 2022; *www.waza.org/priorities/conservation/conservation-breeding-programmes/global-species-management-plans/*)

Widman DR, Abrahamson GC, Rosellini RA. 1992. Environmental enrichment: The influence of restricted daily exposure and subsequent exposure to uncontrollable stress. Physiology and Behavior 51: 309–318.

Wielebnowski NC. 1998. Contributions of behavioral studies to captive management and breeding of rare and endangered mammals. Pages 130–162 in Caro T, ed. Behavioral Ecology and Conservation Biology. Oxford University Press.

Wiese RJ. 2000. Asian elephants are not self-sustaining in North America. Zoo Biology 19: 299–309.

Wiese RJ, Willis K. 2006. Population management of zoo elephants. International Zoo Yearbook 40: 80–87.

Wilcox BA, Murphy DD. 1985. Conservation strategy : The effects of fragmentation on extinction. The American Naturalist 125: 879–887.

Wilson EO. 1988. The current state of biological diversity. Pages 3–18 in Wilson EO, Peter FM, eds. Biodiversity. National Academy Press.

Yerkes RM. 1925. Almost Human. The Century Company.

Young RJ. 2003. Environmental Enrichment for Captive Animals. UFAW Animal Welfare Series. Blackwell Science.

Zinner D, Fickenscher G, Roos C. 2013. Family Cercopithecidae (Old World monkeys). Pages 550–627 in Mittermeier RA, Rylands AB, Wilson DE, eds. The Handbook of the Mammals of the World, vol. 3, Primates. Lynx Edicions.

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