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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

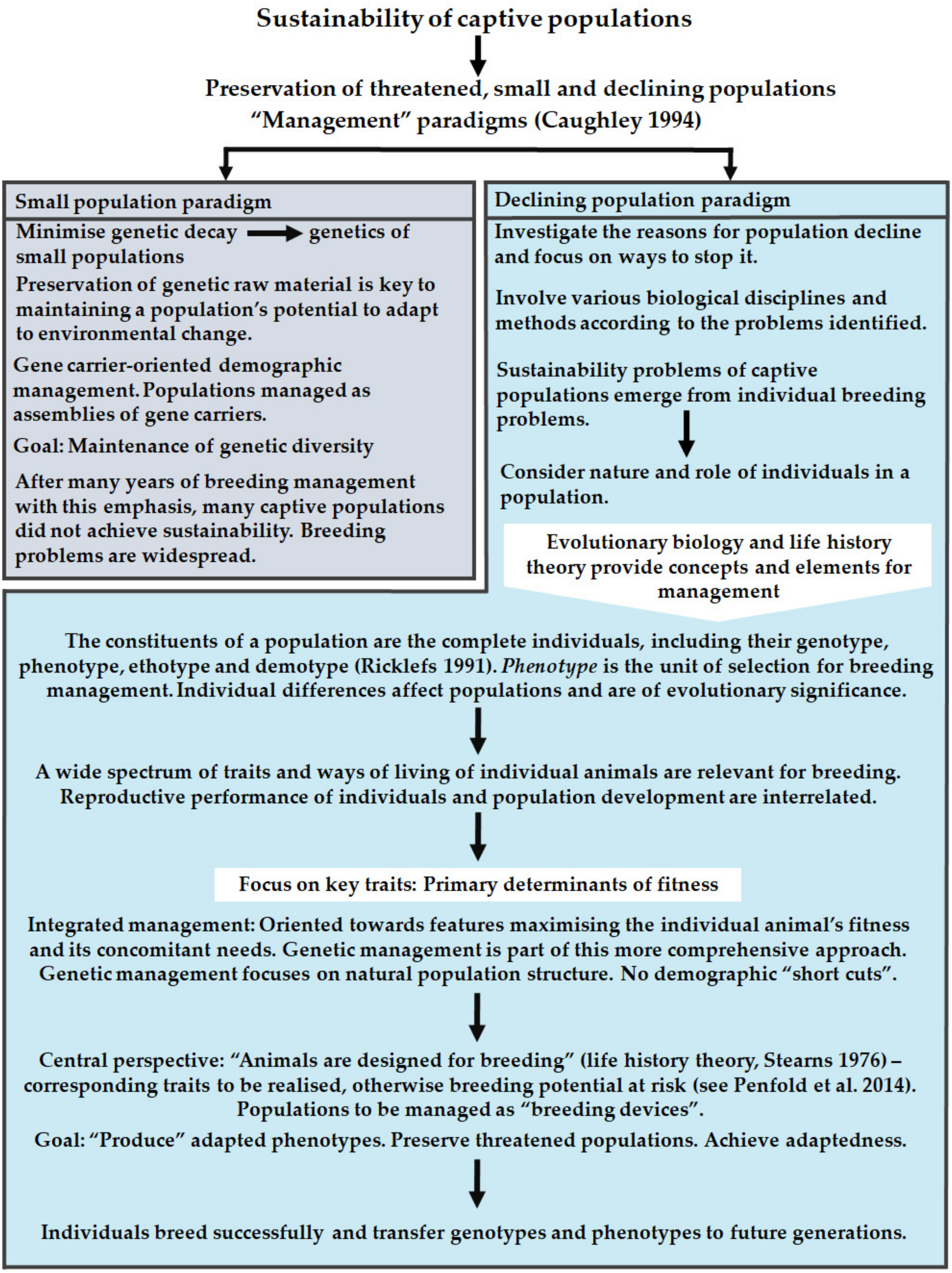

Figure 1. Flow chart of approach.

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.

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