Towards more individual-based and fitness-oriented captive mammal population management

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Many captive populations of birds and mammals are not likely to reach sustainability due mostly to breeding problems. Identifying the conditions under which breeding problems and poor population growth are likely to occur and establishing more appropriate conditions, therefore, will be a necessary prerequisite for future successful conservation breeding and the long-term survival of captive populations. This article analyses the basic approaches and concepts of management programmes for captive mammals. It discusses and propagates an approach which might help increase the productivity of the populations and decrease the risk of viability problems. Evolutionary biology, ecology and conservation biology provide concepts that propose a critical role of the individual phenotype in the context of evolutionary processes, population development and conservation practice. It is assumed that this is not yet sufficiently reflected in the management of captive mammals and possibly other populations, thus contributing to fitness problems. A more individual-based population management that intends to focus on the 'quality' of the individuals and the individual phenotype therefore is proposed. Individuals have to be managed such that they are phenotypically represented in future generations.

Keywords: Adaptive phenotypes, breeding problems, captive mammal populations, units of selection.

A NUMBER of studies in the last years have discussed that many, if not most, captive populations of birds and mammals are not likely to reach sustainability and thus may not function as reserves for the conservation of species[1–5]. For example, the development of the European mammal populations since the 1990s – when many breeding and regional management programmes were started – is characterized by low or even negative population growth in many species and low effective population sizes[4]. On an individual and proximate level, the negative trend often seems to be due to a low mean reproductive output per female and large individual differences in the number of surviving infants – thus indicating fitness problems (see Kaumanns *et al.*[6,7] for captive primates).

In many cases and populations of mammals, living conditions and management programmes are good enough to allow some but – over a long-term perspective – not enough successful breeding. Furthermore, predictability of which individuals are going to breed successfully often is low. This hinders systematic planning. Identifying the conditions under which breeding problems and poor population growth are likely to occur therefore is a necessary prerequisite for future successful conservation breeding and the long-term survival of captive populations. This is also a necessary condition for the realization of plans to achieve 'true sustainability' of zoo populations via more elaborate meta population management, including wild populations[8,9].

The present article assumes that attempts to overcome the current 'viability crisis'[10] would profit from an analysis and discussion of the basic management concepts and paradigms themselves – in addition to ongoing analysis' and discussions of the individual management programmes (see for instance Lynch and Snyder[5]). Management programmes and husbandry procedures indeed are not only based on the individual knowhow of managers, but are also influenced by the underlying basic approaches and concepts. They reflect how the life history, adaptive potential and resulting needs of a species are perceived and therefore can – though indirectly – influence the development of the populations. Critically analysing basic management approaches on the level of methodology and with reference to their validity is also a necessary component of the process of focusing propagation, as recommended by Conway[1]. (See also Walters and Hilborn[11] who propagate an 'adaptive management' for conservation programmes.)

The first aim of this article therefore is to elaborate briefly basic assumptions about the 'nature' of captive mammal populations and possible consequences for their management. The second aim is to propagate a modified

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Box 1. Flowchart of the approach

Populations are constituted by individuals/individual phenotypes (Lomnicki[41]; Sibley and Smith[32]). They are more than assemblies of gene-carriers.

The individual phenotype is where selection acts on. Individuals therefore are the key units of management.

'Individual phenotype' refers to the total of an organism's appearance resulting from the interaction of the genotype and the environment, including all its traits on all organismic levels like morphology, development, physiology and behaviour.

The phenotype comprises several general levels of structure – genotype, phenotype, ethotype (behaviour, physiological processes), demotype (age-specific fecundity, survival values). The transformation processes in live histories (from genotype to phenotype to ethotype, demotype and fitness) are inseparable from each other and have no existence apart from their environmental context (Ricklefs[31]). This complexity and interrelatedness between the different structures within the phenotype and with its fitness needs to be considered and reflected in individual-based population management. A management which reduces the individuals to 'gene-carriers' can lead to maladaptive conditions for reproduction and to viability problems on population level.

The individual is the unit of reproduction. Successful reproduction is a necessary condition for the survival and viability of a population and for the preservation of genetic polymorphism. Individuals contribute to viability by being phenotypicaly represented in future generations – which corresponds to the definition of 'fitness' sensu Stearns). Management therefore in the first line has to provide the individuals with the conditions for successful reproduction. It also should support the production of different phenotypes, since they increase a population's adaptive potential (Carroll and Watters[38]).

Individuals are 'designed for breeding' (Sterns[34]), but management has to establish the conditions which match a species adaptation and especially its fitness-relevant key traits.

Individuals constitute populations and influence their chances to survive via generating species-typical life-history patterns (number of infants per female, date of first birth, group size, etc.). They are relevant for fitness, are shaped by selection and reflect adaptations. They can also act as constraints, limiting the adaptive potential of a species (Stearns[34]). Management should attempt species-typical life-history patterns. Besides others, they provide the proximate conditions for the production of adaptive phenotypes.

Captive populations need to be managed such that they provide optimal living and breeding conditions for the individuals. The various levels on which fitness can be influenced (genetic, demographic, behavioural, etc.) need to be managed in an integrated approach. A population in which successful breeding is established is likely to develop a 'self-sustaining loop' in the sense that adaptive phenotypes are likely to produce further adaptive phenotypes. This would allow 'mapping the genotype into the fitness landscape' (Rickleffs[31]) and support the development of viability and sustainability in a population.

management paradigm based on the results of this discussion and with reference to a broader spectrum of relevant concepts and results of conservation biology. It considers the fragmented and altered nature of captive populations. The article only intends to propose basic components of a conceptual framework, and not to elaborate all of the relevant aspects. It also does not provide husbandry guidelines. The authors are aware that many factors like insufficient population size and structure, suboptimal infrastructural conditions, space problems, organizational problems, etc. can induce viability problems, and therefore do not consider them here. This article discusses the general aspects of a paper that reviewed the development of the global captive population of the lion-tailed macaque (*Macaca silenus*) with reference to its management history, viability problems and the role of individual-based management[12]. Some of the considerations about individual-based management have been outlined already with reference to primate populations[13]. (For a flowchart of the main argument, see Box 1.)

Basic characteristics of captive populations and management approaches

'Populations' of captive animals are established 'virtually' by regarding groups or individuals kept separately in different institutions within a defined area (e.g. a country or continent) together as a unit of management. This 'virtual' population is supposed to have the potential to 'function' similar to a natural population in the wild (for a definition see Brook[14]) – though it represents an extreme case of fragmentation[7]. The 'potential for interbreeding' is one of the key characteristics of a natural population. Under captive conditions it is realized via the local breeding units and a systematic exchange of individuals between them. Depending on their genetic background, different local living conditions, patterns of individual development, and demographic and social background, the individuals of a – often meta-population-like – captive population phenotypically may differ considerably. In an experimental study on oldfield mice, McPhee[15] showed that generations in captivity increase behavioural variance. The specific nature of the captive environment might trigger phenotypic selection over previous generations[16].

The management of captive populations includes husbandry schedules and procedures that under the 'artificial' conditions of captivity (including the almost permanent availability of food and absence of predators) are supposed to keep the animals alive, physically and behaviourally functional and in breeding condition. They include procedures that intend to mimic some of the dynamics found in wild populations (e.g. via establishing new breeding units, transfer of breeding males). Though population management and – on a practical level – especially the routine husbandry in the individual zoos have to refer to many aspects of the life history of animals including their behaviour, sociality, reproduction, etc. demography and genetics are usually regarded as the key levels on which population management has to be carried out systematically[17].

The management of captive populations usually intends to achieve 'sustainability': The number of births should be equal to or larger than the number of deaths[4]. Populations – often derived from a small number of founders – should be 'viable' and especially 'genetically healthy'. In this respect, they should come close to their wild counterparts[17]. Following recommendations and husbandry guidelines of breeding programmes, preserving genetic polymorphism in a population has top priority[4,18,19] and is regarded as a leading paradigm of conservation-oriented population management. In fact, many zoo biologists assume that a population managed such that genetic diversity in the future is likely to remain high can be regarded as 'viable', or will achieve viability. Ballou *et al.*[17], however, point to the possibility that an extreme focus on genetic management can result in a genetically healthy but small or declining population. Viability problems may also arise in a population in which the number of births is equal to the number of deaths, if the deaths include proven breeders (W. G. Conway, pers. commun.).

For management purposes, a set of methods derived from population ecology is used. They refer to, for example, age/sex composition, births, deaths and origin of individuals (wild/captive-born)[17]. These methods, besides others, are used to provide data which allow analysing and predicting the genetic consequences of demographic management with reference to preserving a defined percentage of genetic diversity over a defined period of time (but see Lacy[2] for a critical discussion of this approach). The availability of these methods 'packed' into a comfortable management software with the capacity to provide such predictions seems to facilitate that management decisions in breeding programmes indeed are often taken under the perspective of their genetic consequences in the first line. The individuals in a population thus are likely to be predominantly perceived and managed as 'gene carriers', the sum of which ideally should represent the genetic diversity attempted.

Gene carriers versus individuals

This article assumes that the approach outlined above needs to be discussed critically. Expanding Ballou's[17] notion (see above), it is postulated that a strictly executed genetic management sometimes influences breeding programmes and management procedures, such that other ('non-genetic') aspects that are part of life histories of animals as well are at risk to be neglected. This possibly (in the long run) can lead to maladaptive living conditions, especially with reference to the functioning of the reproductive system and the potential to reproduce successfully[10]. There seems to be indeed a tendency not to notice that the 'gene carriers' in a population have to be 'produced' by the 'complete' organism (phenotype), many traits of which are functional on a proximate level for its survival and reproductive performance – but not to be covered directly by genetic management. Social skills, for instance, which are acquired during socialization (usually under specific management-induced social and demographic conditions), can decide about whether an important 'gene carrier' reproduces. The role of such critical aspects in influencing the development of a population, especially in terms of achieving successful breeding overall, may not yet be considered enough – though a number of authors point to the importance of, for instance, behavioural knowhow and behavioural components in management programmes[20]. The interest in the individual animal and its behaviour is also reflected in a growing number of studies and programmes emphasizing the importance of personality traits and related phenotypic traits. These studies also point to the need to consider animal welfare together with personality traits for population management[21–25]. In some of the definitions used for 'personality'[24,25], the latter term is almost synonymously used with 'individual and its behaviour'. According to Watters and Powell[24], animal personalities are supposed to affect the conservation mission of zoos, both directly and indirectly. These authors, however, state that incorporating knowledge of animal personalities has so far mostly been done on a case to case basis.

Evidently genetic management as such is a necessity: conservation genetics generated an impressive and indispensable body of scientific knowledge for population management[26]. Problems are likely to occur, however, when the fitness-relevant genetic management is carried out without the support of and control by an equally valid and evolutionary based set of management tools dealing with the equally fitness-relevant factors that are beyond the scope of genetics[27,28]. This, besides others, may also refer to epigenetic phenomena which, according to Bateson and Gluckman[29] 'usually refers to what happens within a developing individual organism'.

Populations are constituted by individual phenotypes

Populations are constituted by individual phenotypes[30]. Population management therefore has to refer to the individual as a whole and should not be genotype-biased. The genotype is ('only') one of the structural levels of the phenotype[31] and consequently, there is a need for population management to consider the genotype together with the other levels in order to develop a balanced management approach. The term 'phenotype' refers to the total of an organism's appearance resulting from the interaction of the genotype and the environment and includes its traits on all organismic levels like morphology, development, physiology, and behaviour. According to Ricklefs[31], 'the thread of causation between genotype and fitness passes through general levels of structure – genotype, phenotype, ethotype (the behaviour, including physiological processes, of the organism) and demotype (the age-specific fecundity and survival values). 'The transformation processes in life histories (from genotype to demotype and fitness) are inseparable from each other and have no existence apart from their environmental context. Each component of the structure of the life history, at each level of its hierarchy, inter-relates with other components and with fitness'[31]. It is especially this complexity and inter-relatedness of life histories which ask for a better 'representation' in population management. To achieve this, and since the individual phenotype is the unit on which selection acts[32], a more individual-based and phenotype-oriented population management is proposed. While incorporating genetic aspects, it should predominantly aim at 'producing' adaptive phenotypes via the establishment of living conditions that enable the individuals to reproduce successfully. They thus and only then can provide the necessary conditions for preserving the degree of genetic polymorphism attempted. The 'degrees of freedom' for genetic management, however, would be defined by the requirements set by the social and reproductive system of the species with their corresponding adaptations and constraints, and by the specific genetic, demographic and social conditions available in the population to be managed. In fragmented and altered wild populations of mammals in principle similar constellations, limitations and management requirements can be found (see below).

Individuals in a population

A change of paradigm towards more individual-based population management as suggested is indicated also to mimic more closely the role of an individual in natural populations as investigated by life-history theory: the individuals in a natural population not only 'constitute' the latter demographically and genetically, via the 'interface' of generating species-typical life-history patterns (e.g. within a certain range females give birth to a certain number of infants in certain time intervals in groups with a certain size and composition), individuals influence a population's chances to survive. (For life-history trade-offs and the evolution of animal personalities, see Wolf *et al*.[33]) Life-history theory demonstrates that these patterns are relevant for fitness[34]. They are shaped by selection; they reflect adaptations that are solutions to recurrent problems of survival and reproduction, and may also act as constraints. The latter limits the adaptive potential of a species and can lead to fitness problems when ignored by population management. It is therefore crucial for the management of both wild and captive populations to consider and establish links between the individual and its behaviour on the one side, and population size and composition on the other side[35–37]. To ignore the individual and individual phenotypic variation respectively, means ignoring factors that influence the viability of a population[38]. Gosling[39] indicates that in this respect, the behaviour of individuals in small populations is relatively more important than in larger ones[40]. The focus on the individual as a whole and its living conditions also was propagated earlier by Lomnicki[41], who suggested not to look at the average individual for the study of population dynamics, but to look for differences between the individuals and to investigate how these differences affect their reproduction and survival (see also Watters *et al*.[16]).

An individual's chances to survive and to reproduce successfully – its fitness – on the other side are influenced by the demographic and social structures in groups or other units of reproduction and in local subpopulations within a population[42,43]. These structures as well as the schedule and timing of key events in the lifetime of an organism (e.g. age at first birth, number of offspring, group size, mating system) refer to species-typical adaptations (e.g. specific social structures). They provide the conditions for optimization of reproductive processes and output to the individual. For example, in a set of genetically related adult females of a female-bonded species like the lion-tailed macaque, the individual females may be more productive when kept in one large one-male group (preferably their natal group with well-established social bonds) than when split up and kept in various (different) small groups. However, keeping them in different groups with genetically different breeding males would be preferable under the specific perspective of genetic management.

The proposed individual-based management paradigm is in accordance with a recently proposed research paradigm propagating individual-based models in population ecology[44]. It is based on the assumption that ecological dynamics, including demographic rates are arising from how individuals interact with their environment and with each other[32]. It assumes furthermore that underlying behavioural decisions themselves are based on fitness-related decision rules[45]. Consequently, individual-based models to predict aspects of the development of populations are propagated[44]. They, for instance, provide insights into how populations made up of social groups have dynamics, and ultimately persistence, determined by individual behaviour[46].

Captive populations are fragmented and altered populations

This article assumes that viability problems are also basically influenced by the fact that individuals in captive mammal populations usually live under highly fragmented and altered conditions. It is likely that the latter can rarely provide optimal living and breeding conditions[47] – a problem wild populations are also confronted with more often[48–52]. Management programmes for captive mammals have to explicitly consider the limits resulting from this[7]. It is likely that captive conditions can result in a decrease in fitness as indicated by breeding and viability problems on the individual and population level[10]. This phenomenon can be discussed as a consequence of 'Allee effects'[53,54]. According to Allee, many animals suffer a decrease in per capita population growth rate when population density reaches a low level. Several studies on Allee effects and their relevance for the conservation of plant and animal species have been published recently with reference to wild populations and in the context of reintroductions (for an overview, see Courchamp *et al.* [54]). The importance of Allee effects for the management of captive mammal populations is discussed by Swaisgood and Schulte[55]. According to Courchamp *et al.*[54], captive populations might be specifically prone to Allee effects triggered by deficits in 'reproductive facilitation'. Studies on the causation of Allee effects (e.g. Somers *et al.*[56]) indicate that factors related to individual behaviour play an important role.

Zoo biologists so far rarely discuss the altered and fragmented nature of captive populations (but see Swaisgood and Schulte[55]), though many traits of the individual populations influenced by this are fitness-relevant and may possibly induce viability problems (but see Lacy[2] for more elaborated meta population management that would also include such aspects). Since the search for solutions of viability problems inevitably has to trace them back to individual breeding, a better theoretical and practical integration of the individual and its behaviour into population management is crucial also from this end (see also Coté[36]).

An evolutionary-based concept for the integration of behavioural knowledge into conservation practice has been propagated by Carroll and Watters[38]. It contributes to the development of integrative management concepts both for altered and fragmented wild and captive populations and also propagates a 'phenotype-oriented' approach. According to Carroll and Watters[38], 'intense management of phenotypes can enhance effective population size and thereby protect viability and genetic variation'. Phenotype management is consequently also propagated for habitat restoration, which can provide the environmental conditions for the development of phenotype diversity[16]. It seems likely that this approach would also fit for captive environments and specifically for the design of enrichment programmes.

According to Carroll and Watters[38], individual-based and phenotype-oriented management emphasizes that adaptation under rapidly changing and altered living conditions is more likely to occur under conditions of sufficient 'phenotypic variability'; that is, when a variety of types of individuals and a variety of traits in which individuals differ provide a larger spectrum of solutions to the emerging problems[23,57,58]. To 'produce' this variety of types under captive conditions probably would require more diversified captive living conditions (including for example, multi-group keeping systems) than what is usually recommended by husbandry guidelines with their tendency to standardize. A large spectrum of social, ecological and cognitive aspects have to be considered. Overall, however, the meta population character of many captive populations with their many different local conditions might, if it occurs, rather trigger scattered than directed selection and provide a fuller view of the phenotypic potential of a population (J. V. Watters, pers. commun.). An important aspect that tends to be neglected often (especially in primates) are intergroup relationships (e.g. via group encounters) for the development of species-typical social dynamics. They are relevant, for instance, with reference to exchanges of breeding males, to allow mate choice, and overall for the development of social skills[59].

Individual-based and phenotype-oriented management is organized towards successful reproduction

Successful reproduction is a necessary condition for the survival of a population. The individuals are supposed to contribute to the viability of population by successfully reproducing and thus by being phenotypically represented in future generations. Following Stearns[60], the latter can be regarded as a definition of (or expression of) 'fitness'. Fitness in this perspective is what captive management has to go for. Population management consequently and in the very first line has to establish the conditions for successful reproduction in species-typical breeding units – and not only to produce offspring or specified gene carriers. It also has to maintain the potential for successful reproduction – especially when reductions in population size, e.g. via birth control measures are practised temporarily. Since successful reproduction depends on the 'quality' and especially the behaviour of individuals and on the 'quality' of the breeding units, the size, composition, and demographic structure of a captive population have to be defined and developed from this end[12,13]. The various levels (genetic, demographic, behavioural, etc.) on which fitness can be influenced via specific management procedures need to be adjusted, outbalanced and integrated towards successful breeding. Such an integrated population management would intend to mimic the complexity of factors triggering life-histories, population dynamics, genetic architecture and fitness in natural populations. Systematic control and manipulation of, for instance, selective processes, phenotype development, etc. however, are difficult if not impossible to achieve. To minimize the risk of inappropriate management a 'fine-tuned adaptive management' sensu Walters and Hilborn[11], which continuously and sensibly assesses the effects of management procedures, especially with reference to maintaining the breeding potential is required. It would be against the logic of individual-based and fitness-oriented management to fix the (target) size and structure of a captive population a priori and with reference to available spaces only. It rather needs to be worked out first under which conditions – especially with reference to optimization of individual reproductive output – the population would achieve viability and function as outlined above by referring to fitness-relevant key traits (sensu Carroll and Watters[38]). Due to their small size alone for many captive populations and species respectively, the necessary conditions may not be available[8]. Population management also has to explicitly consider how to prevent Allee effects and whether the projected size and structure have to include a 'buffer' against the risks of stochastic effects on the level of genetics and especially on the level of demography[14]. In particular, with reference to these effects, the reproductive output of the individuals and of the breeding units needs to be monitored continuously and analysed with reference to the development of effective population size over time[61,62].

Life-history theory assumes that animals are 'designed' for breeding[34,60]. Successful reproduction requires – besides the 'necessary' individual traits and skills – living conditions that correspond to their 'design'. On a population level and on a larger timescale, appropriate conditions would be reflected in the emergence of species-typical key events and life-history patterns. Life-history patterns and related adaptations evolved as a means of maximizing reproductive output[34]. To manage a captive population towards achieving the species-typical life-history patterns is of utmost importance, since necessary demographic and other patterns provide the individuals with the proximate conditions for the 'production' of adaptive phenotypes – that is, of individuals breeding successfully. For example, in the case of primates and social carnivores, this besides others, would especially include the establishment of demographic and social conditions for the appropriate socialization of individuals.

The importance of fitness-relevant key traits

There are many factors that determine the fitness of an individual and a population (for an overview, see Rockwood[63]). Beyond the level of providing the means for physical 'survival' (appropriate food, climatic conditions, etc.), managers have to work out which of the factors and especially which traits require special emphasis. A key trait is a primary determinant of fitness in a given condition[38]. Key traits relevant to population management evolved in a number of different functional areas of an organism: they might refer to a species feeding ecology, predator avoidance, social life and others. Many of such adaptive patterns and systems are conservative and inflexible and act as constraints, especially on social interactions, mobility and the reproductive system[64].

It is likely that the viability and sustainability problems in many captive mammal population besides others are a (long-term) consequence of ignoring species-typical adaptations. For example, suboptimal keeping systems and by inappropriate social and demographic conditions in the breeding units thus leading to *low* individual reproductive output. The latter in the long run may trigger effects (e.g. unfavourable age/sex structure) which influence viability negatively. There might be breeding, but not enough in the long run.

Conclusion and consequences

The discussion of the currently used basic approaches towards population management in captive mammals revealed the need for modifications which contribute to more productivity and help avoid viability problems. Evolutionary biology, ecology and conservation biology provide concepts that propose a critical role of the individual phenotype in the context of evolutionary processes[34], population development[30,37] and conservation practice[38]. This is not yet appropriately reflected in the management of captive populations. A more individual-based approach with a management that intends to focus on the 'quality' of the individuals and their potential for breeding in a population – therefore is indicated. It seems that problems in the current management approaches are especially found with reference to 'mapping the genotypes into the fitness landscape'[31]. Whereas the genotype-structure of the individual phenotype is systematically addressed as a unit of management, the ethotype, comprising the behavioural and physiological manifestations receives less systematic attention. In particular, population management may lack an integrated approach towards achieving fitness by providing conditions that allow individuals to breed successfully and to be phenotypically represented in future generations. Watters and Powell[24] provide valuable suggestions and concepts for an expanded population management that besides others would incorporate behavioural type data and which therefore support the approach of the present article. A management software that would support managers to deal with the complexities of a phenotype-based approach is missing so far. It might refer to an initiative by Deans *et al.*[65] to develop a computerized database 'to understand the vast landscape of phenotypic data'.

A change of paradigm towards more individual-based management does not implicate treating or even manipulating the individuals in a population in a way which principally differs from the one used so far. Good managers always take care of individuals[24]. The novel approach rather suggests to predominantly characterize and manage a population under the perspective of the patterns of reproduction on the level of the individuals, their breeding units, and on population level, over as long time periods as possible. Since the reproductive output is a 'product' of the individual phenotypes, their 'status' and its management on a proximate level have to be the main focus. Individual-based and fitness-oriented management almost 'by definition' provide the genuine conceptual frame for the integration and realization of management and husbandry measures referring to personalities and welfare of the animal[24,25]. Dawkins[66] has elaborated the relationships between individual 'motivation', animal welfare and fitness.

Attempts to solve the 'viability crisis' referring to the considerations outlined above would require larger populations, significant improvements of breeding conditions and much more breeding – once it 'works'. The latter is important to achieve a 'critical mass' of adaptive (reproductively competent) individuals that help avoiding Allee effects[10]. Larger populations are also required for programmes that intend to contribute to species reintroductions, since mortality can be high. The spatial and economical requirements to realize this probably would be on a scale and in an order of magnitude that could be realized only for few species and populations respectively. A serious reduction in the number of species kept in zoos, as propagated since decades by Conway[1], would be inevitable.

Conde *et al.*[8] provide an overview of the populations of wild animals kept in zoos globally, that might be used for conservation breeding via meta-population management. They however, also outline the enormous efforts necessary to use this potential. It is likely that – looking at the 'quality' of the populations – only a small proportion of them has the potential to play a significant role in the context of the 'one-plan approach'[9] (see also Alroy[67]). It will be an important challenge for the zoo community to identify these populations soon, but also to clarify the role of the many other populations for conservation.

Both conservation biologists working with fragmented and threatened wild populations, and biologists working with captive populations are facing similar problems. An integrated (meta-population) management approach would require that both sides consequently refer to concepts of evolutionary biology as demonstrated by, for example, Carroll and Fox[52] and Schulte-Hostedde and Mastromonaco[68].

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