



EDITED BY

Honnnavalli Kumara

Salim Ali Centre for Ornithology and Natural History, Coimbatore, Tamil Nadu, India.

*CORRESPONDENCE

Nilofer Begum

✉ niloferbegum3@gmail.com

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Wild animals in zoos: A new paradigm is needed for zoos in the future

Werner Kaumanns¹, Nilofer Begum^{1*} & Mewa Singh²

¹LTM-Research and Conservation, Eschenweg 5, 37130 Gleichen, Germany

²Biopsychology Laboratory, Institution of Excellence, University of Mysore, Mysuru, India

Abstract

This review describes the main approaches used for working with wild animals in zoos, and briefly traces the history and theoretical background of these approaches. The theoretical background should be considered when current approaches are discussed for the improvement and design of future zoos. Hediger's individual-based concept of 'Zoo biology' is introduced, followed by a (small) population-oriented approach. Further approaches are presented focusing on animal welfare and behavioural/environmental enrichment concepts. We found that for all approaches, there is a lack of consideration of concepts of evolutionary theory. Lacking these concepts and the divergent backgrounds of the approaches might account for the management and resulting sustainability problems. Recent management concepts that are based on evolutionary theory, particularly life-history theory, are proposed. The use of these concepts requires a change in paradigm in terms of focusing management and husbandry on the individual phenotypes (the units of natural selection) that constitute a population, instead of focusing on populations as assemblies of genotypes. It is proposed that a paradigm change can support the development of a comprehensive and integrated management approach that would be more compatible with all critical aspects of the biology of the animals and treat them on the same level of importance. Since reproduction is central to evolutionary theory, the new paradigm would particularly emphasise the management of the reproductive biology of the species, and thus support breeding.

Keywords: *Ex-situ* conservation, future zoos, individual-based, management concepts, phenotype-oriented, zoo animals

Introduction

Keeping wild animals in zoos has a long tradition. After an early period, in which wild animals were kept for entertainment and out of interest for foreign worlds (see Gray, 2017), a 'science-based' and more animal- and conservation-centred period followed. In the earlier period, the quality of the living conditions and welfare aspects were not considered systematically. Discrepancies between natural habitats and the altered conditions in zoos, as well as the resulting suffering of the animals and mismatches, were perhaps not considered, or even understood. During the science-based period that started in the 1950s, new approaches to working with wild animals in zoos were propagated, which resulted in better living conditions, higher survival rates, and more successful breeding. Scientific standards with biology-based husbandry techniques and guidelines were developed. Starting from 1980s, an orientation emerged towards regarding individual animals as parts of a population, with the aim to establish captive populations of a species as a reserve for its threatened wild populations. This development brought zoo biology closer to conservation biology. As a consequence, many captive populations were managed under breeding programmes. The potential for long-term persistence and sustainability of these populations, however, turned out to be low in many of the cases (see Lees & Wilcken, 2009; Lacy, 2013; Powell *et al.*, 2019a) – possibly due to prevailing suboptimal husbandry and population management and a lack of integrated management involving conservation planning (Lacy, 2013). The need for improvements in husbandry and management was discussed subsequently by several authors (see the special issue of *Zoo Biology*, Vol. 38, Issue 1- Powell *et al.*, 2019b).

Our study emphasises that management approaches are influenced by various considerations and 'philosophies' that emerged in the history of zoos. These philosophies influence the approaches currently used and, therefore, must be considered when these approaches are discussed critically. It is the aim of this paper

to describe the main approaches used for the work in zoos, and to consider their potential to establish an integrated management approach sensu Lacy (2013), for the viability of captive and all populations that are interactively managed or affected.

Hediger's 'Zoo Biology'

The first comprehensive and influential concepts about the work in zoos were developed by Hediger (Hediger 1942, 1950, 1954, 1968, 1965, 1969, 1982, 1984). According to him, concepts as available at the beginning of the 20th century did not consider the *principal* aspects of keeping wild animals but only consisted of *individual recipes* and recommendations. As a general principle, he proposed to consider keeping wild animals in zoos with reference to the seemingly trivial fact that the natural living conditions of an animal differ from those in a zoo. The differences should be identified and bridged. Husbandry should be designed by using information about the biology of the species and should focus on the individuals. The work in zoos, overall, should be science-based. To achieve this, he proposed to establish a special biological discipline called 'Zoo biology'. Within the zoo biology framework, various disciplines should function interactively towards dealing with three main clusters of problems: space, nutrition, and the animal-man relationship (see Hodges *et al.*, 1995). Hediger proposed that zoo biology covers anything that is of biological relevance in a zoo (Hediger, 1965, 1969). According to Chrulw (2020), Hediger's theoretical position is established from the perception of the world from the animal's point of view. The concept of a 'self-world of the animal', as used by Hediger, was elaborated earlier by a theoretical biologist Jakob von Uexküll (von Uexküll, 1920, 1926, 1957; Uexküll & Kriszat 1934). Chrulw (2020, p. 137) notes that Hediger 'operationalised' Uexküll's approach to animal worlds in order to optimise the design of zoo enclosures. The enclosures are considered as both physical and psychological habitats in which captive animals could live appropriately. For instance, enclosures that could function as a 'territory' and allow critical 'flight distances' would be ethically and biologically acceptable. Properly equipped enclosures in zoos would support the animals' well-being and allow a long life and successful reproduction, an indicator of the appropriateness of the keeping system. As an important means to facilitate coping after the transfer of an animal from the wild to captive conditions, appropriate habituation and training procedures to achieve 'tameness' are suggested. Continuous training would furthermore keep the animals busy and prevent behavioural disturbances and boredom. Hediger's recommendations were derived from personal observations and experiences. They are based on knowledge of the biology of the species involved, as available in the 1960s. These recommendations are still applied and cited as founding elements for welfare and enrichment concepts (Shepherdson, 1998; Maple & Perdue 2013; Powell & Watters 2017). His later publications, especially his book '*Beobachtungen zur Tierpsychologie im Zoo und im Zirkus*' (Hediger, 1961), however, indicate that he was not aware of, or was reluctant to integrate some developments from animal behaviour studies (comparative ethology, sociobiology) into his concepts of the work in zoos. He rather cultivated an approach that neglected standards of scientific work and ignored the theory-based, experimentally oriented, and quantitative approach of some relevant disciplines. Under the umbrella of a '*Tierpsychologie*' (animal psychology) that intends to 'understand' ('*Verstehen*') an animal's behaviour, he made use of anthropomorphic and speculative explanations, *e.g.* concerning animal-man relationships (see Hediger, 1961). The evolutionary theory was not considered sufficiently. Hediger rather regarded the discrepancies between the living conditions in the wild and in

captivity as a key aspect of the work in zoos, but did not consider them in (theoretical) terms of the adaptive potential of a species, thus neglecting an important concept of evolutionary theory (see Hediger, 1982).

After Hediger's publications, Kleiman *et al.* (1996), for the first time, provided a comprehensive description of key topics and approaches used for the work in zoos in their book 'Wild Mammals in Captivity'. Kleiman *et al.*'s approach was based on Crandall's (1964) work, which itself was appreciated by Hediger (1965) as the first "*Lehrbuch der Wildtierhaltung*" (Textbook for Keeping Wild Animals). Crandall's approach was strictly organised along the taxonomic units of mammals, whereas the contributions of Kleiman *et al.* (1996) are organised with reference to various functional clusters like 'basic husbandry', 'nutrition', 'exhibitory', and 'population management for conservation'. A more recent comprehensive overview of research activities and key topics carried out with reference to zoos is provided in Kaufman *et al.* (2019). Many of the studies cited there are published in 'Zoo Biology', a journal that covers a large spectrum of topics following Hedger's eclecticist approach. It was regarded by Hediger (1982) as a visualisation of his concept of zoo biology. Wemmer *et al.* (1997), Anderson *et al.* (2008), and Lindburg (2008) provided analyses of the topics covered in Zoo Biology, and their studies indicate a bias towards dealing with mammals, and especially primates, and their behaviour.

Change in paradigm: Populations matter for conservation!

The topic 'population management' in Kleiman *et al.* (1996, 2010) refers to an important paradigmatic change in the role of zoos and work emerging in the 1980s. The *wild* populations of zoo conspecifics were increasingly perceived as endangered, and the zoos were supposed to think beyond individual institutions and support the species' survival by establishing *reserve populations*. They were also supposed to support relevant research, field studies, and conservation projects in the countries of origin. The national and international breeding programmes taken up in the 1980s enriched the work in zoos by introducing coordinated management between individual zoos and advanced, science-based husbandry standards, especially in terms of genetic management. In the breeding programmes, the individuals of a species kept in different zoos were 'virtually combined' into a population that was supposed to serve as a reserve, a model, and an ambassador for the wild population. The programmes introduced concepts of population biology and, referring to the usually small size of zoo populations, preferably used concepts of the genetics of small populations (see Ballou *et al.*, 2010). The long-term persistence of captive populations of a species and the realisation of its function as a reserve were believed to depend mainly on management aimed at the preservation of genetic diversity. The members of a population were expected to transfer the 'genetic raw material' to further generations (Ballou *et al.*, 2010). The number of species covered by breeding programmes has grown rapidly in the last decades, but many of these captive populations so far have not been productive enough to develop the potential for sustainability (Leus *et al.*, 2011; McCann & Powell 2019).

Back to individuals: Focus on animal welfare

Parallel to, and rather independent of, the establishment of captive populations with its focus on the genetic management, the issues about the quality of life of individuals and their captive environments generated renewed discussions

(Shepherdson, 1998; Melfi, 2009). As elaborated by Powell & Watters (2017), these discussions were forwarded by animal welfare movements in Europe and the USA, referring to the wellbeing (and suffering) of animals in a variety of contexts and institutions in which wild or domesticated animals were kept under suboptimal conditions. According to the authors, the zoos, and especially the zookeepers, gave consideration to the welfare matters. Aspects of the life of individual animals and their traits got back into the focus of management, thus turning back to Hediger's approach. This was also possibly induced by the widespread breeding problems in many programmes (see Powell *et al.*, 2019a). As means of choice to improve welfare since the 1990s, 'environmental' or 'behavioural enrichment' measures and programmes were propagated (for definitions see Shepherdson, 1998). Many publications and projects related to the above issues were launched (see Young, 2003; Kleiman *et al.*, 2010; Maple & Perdue, 2013; Binding *et al.*, 2020). Some authors have even 'upgraded' and treated these fields of work, especially the topic of animal welfare, as independent 'sciences' (see Maple, 2007; Powell & Watters 2017). It seems that this approach tended to 'displace' the function, scope, and importance of 'ordinary' husbandry and management. A few authors (Schulte-Hostedde & Mastromonaco, 2015; Bacon, 2018), however, emphasise the need to integrate enrichment measures into general husbandry and management.

Current welfare, as well as enrichment concepts and projects, differ in terms of their 'philosophical background'. According to Mellen & MacPhee (2001), they have been influenced by different 'schools of thinking' resulting in 'behavioural engineering' (Markowitz, 1979, 1982) and a 'naturalistic' approach (Hancocks, 1980; Hutchins *et al.*, 1984). Mellen & MacPhee (2001) proposed a 'holistic approach' based on the assessment of the animal's natural history and exhibit constraint, and providing species-appropriate opportunities.

Enrichment and animal welfare concepts have been influenced by concepts of early comparative psychology and behaviourism, respectively, as represented by, for example, Watson (1928), Skinner (1974), and Erwin *et al.*, (1979). Guided by a rigid research paradigm, these researchers carried out experimental studies (*e.g.* on learning) using animals kept under strongly controlled and therefore often 'barren' conditions that explicitly ignored species-typical traits, corresponding adaptations and welfare considerations (see also Shepherdson, 1998). One of the proximate consequences of this approach was that the experimental animals developed behavioural disturbances and bizarre behaviours (*e.g.*, Skinner, 1948; see also Novak *et al.*, 2006). They sometimes could be 'treated' and 'healed' by providing a richer spectrum of environmental and/or social stimuli. These studies influenced the establishment of the currently used 'enrichment' concept with its focus on specific critical stimuli and limited consideration of the overall living conditions.

The critical phenomena that are addressed to develop 'enrichment' measures and to assess their effects are aspects of an individual animal's behaviour, but also of its physiology, and more recently, of the cognitive and emotional system. 'Stress' is regarded as one of the key management and research problems in this context. According to the 'behavioural engineering' approach influenced by Markowitz (1979, 1982), the animals are predominantly considered in their *artificial* environment with regard to potential mismatches to the internal status of animals (*e.g.* resulting from a need or drive to migrate, to hunt for food or to lead a social life). A *naturalistic* approach (see Hancocks, 1980) aiming at animal welfare considers the animal predominantly in its natural environment. Captive conditions should allow the realisation of species-typical behaviour. This approach comes close to Hediger's concepts and seems to fully realise 'animal welfare' considerations. Living

conditions of animals in their natural habitat, however, usually cannot be perfectly replicated in a zoo due to space limitations and other constraints. Naturalistic approaches, therefore, also may have to consider whether the 'naturalistic' conditions offered in a zoo really meet the needs of animals and their adaptive potential (see Poole, 1992).

Studies emerging from a comparative/behaviouristic background typically use terminology and concepts of behaviourism. The lack of concepts of evolutionary biology and the concept of species *adapted* to special environmental conditions and life history patterns in the behaviouristic approach can limit the potential of this approach for the development of appropriate husbandry and management programmes.

The various approaches and concepts as outlined above have divergent theoretical and methodological origins. Hediger (1954, 1968, 1984) saw his work in the context of biology, animal psychology, and veterinary medicine. His '*Tierpsychologie*', however, had a very personal and anthropocentric perspective and was not close to the 'Comparative Psychology' with its behaviouristic background as used in the American science community. Further, it was not compatible with the quantitative and hypothesis-oriented comparative ethology that substituted '*Tierpsychologie*' in Europe.

The population-oriented work in zoos that emerged in the 1980s was not derived from Hediger's concepts. It emerged from thinking in terms of (threatened) populations, as emphasised in conservation biology. It, however, does not consider the full spectrum of concepts of population ecology. It is rather guided by concepts of the 'genetics of small populations', focusing on the individuals of a population in their existence as genotypes and is mainly organised in the frame of the 'small population paradigm' (see Caughley, 1994). It led to a reduced consideration of the nature of the individuals and of the captive populations, and its foundation in evolutionary theory. The individuals are managed mainly with reference to their existence as gene carriers - although the genotype of an individual represents *only one of the levels* of the individual phenotype. To achieve defined genetic structures in breeding units and populations, the 'small population paradigm' propagates demographic management with a strong focus on the genotype of individuals - as derived from pedigrees - ignoring or overruling (adaptive) traits of the reproductive system of a species including 'non-genetic traits' that are critical for successful reproduction (see Hildebrandt *et al.*, 2000; Hermes *et al.*, 2004; Wachter *et al.*, 2011; Ludwig *et al.*, 2019).

The animal welfare and enrichment movement contributed to the establishment of programmes and husbandry schedules that improved the quality of life of animals in zoos. Its origin in behaviouristic concepts, which ignore species-typical traits, however, can hinder an integration of aspects of biology of an animal, like adaptations as evolved in the past and acting as constraints and factors that determine a species' potential for dealing with altered living conditions.

Recommendations for husbandry and management derived from diverging approaches may not sufficiently support each other and lead to unbalanced keeping and management systems. Discrepancies, for instance, may occur between recommendations concerning aspects of genetics and behaviour. Sustainability problems in many captive populations, as currently described (Kaumanns *et al.*, 2008; Lees & Wilcken, 2009; Leus *et al.*, 2011; Long *et al.*, 2011; Che-Castaldo *et al.*, 2019), may be a consequence of such discrepancies. It is assumed that a comprehensive and integrated approach requires the consideration of the key traits of the species involved along with relevant concepts of evolutionary theory,

especially those that concern with the persistence and adaptability of populations. Lacy's (2013) proposal of a management that integrates the various levels of husbandry and other parts of the work in zoos under the umbrella of pedigree-based genetic management is critically regarded. It is rather assumed that the various areas of husbandry and management of captive populations can only be integrated by referring to their common background as provided by evolutionary-based biology. Evolutionary theory does not support the dominance of one area (*e.g.* genetics) as a guiding discipline for husbandry and management. Its appropriate consideration would rather promote a balanced approach covering all aspects of an animal's life on the same level of importance.

Elements of a broader approach: Individual-based and phenotype-oriented

The 'classical' approaches are not fully based on evolutionary theory, or inadequately consider relevant concepts. Some authors, however, propagate the integration of evolution in the management of captive zoo populations (*e.g.*, Seidensticker & Forthman, 1998; Schulte-Hostedde & Mastromonaco, 2015). They demonstrate how this can enhance reproductive success and health for sustainability by using, for example, the integration of the natural mating system in the management of a captive population.

Based on the assumption that breeding and managing animals in zoos must incorporate all basic aspects of their biology, an integrated approach to husbandry and management requires a common foundation in evolutionary theory. Therefore, we propose a new approach by using the relevant concepts of evolutionary theory, especially life history theory, as a basic and guiding framework. For the practical work in zoos, this would require a change in paradigm in terms of regarding the individual phenotype as the key unit of management, and not the population to begin with. It would lead to a more appropriate consideration of an animal's complex biology and resulting needs. It especially should lead to more emphasis on the management of the reproduction – the core biological system in evolutionary theory.

In a series of papers, Kaumanns *et al.*, (2013, 2020) and Kaumanns & Singh (2015) propose the basic elements of an approach with regard to the prevailing approaches. With reference to life history theory, they argue that populations are constituted by individual phenotypes and not just by the latter's genotypes. A key component of life-history theory is that individual phenotypes are the constituents of a population and are therefore under selection (see Ricklefs, 1991; Stearns, 2000; Hendry *et al.*, 2011). According to Ricklefs (1991), the transformation processes in life histories from genotype to phenotype to ethotype (behaviour, physiological processes), demotype (age-specific fecundity), and fitness are inseparable from each other and have no existence apart from their environmental context. This complexity and interrelatedness among the different structures within a phenotype and its fitness must be considered and reflected in individual-based population management (see Kaumanns & Singh, 2015). Such an approach must regard the individual phenotypes as the units of management. The individual phenotypes in a population and the population are interrelated. 'Individual phenotype' refers to the total of an organism's appearance resulting from the interaction of the genotype and the environment, including all of its traits on all organismic levels like morphology, development, physiology, and behaviour (Kaumanns & Singh, 2015). Regarding individuals as the units of management with all their fitness-related properties that contribute to individual variation

in survival and reproductive success requires the establishment of a management approach that considers their various properties (genotype, ethotype, demotype) at the same level of importance (see Kaumanns *et al.*, 2020). The various fields of practical management and husbandry should be organised accordingly. The management of behavioural traits, for example, is as important as the management of genetic systems. It is evident, however, that under the limited captive conditions, it can be difficult to outbalance, for instance, the requirements resulting from these systems (see Ballou *et al.*, 2010; Kaumanns & Singh 2015). Compromises must be developed that allow coping within the frame of the adaptive potential of the species and within the coping potential of an individual on the level of modifications (*e.g.* learning) (see Kummer, 1971). Watters *et al.*, (2003, 2017) propagate and elaborate a phenotype-oriented approach to population management. They, however, do not explain how this would be compatible with the widely used 'classical' demographic approach as emerging from the small population paradigm.

In addition to emphasising the need for phenotype-oriented management, Kaumanns *et al.*, (2020) point to a greater consideration of the reproductive system of a species. This is indicated by the life history theory, which states that the adaptiveness of a population is realised *via* the successful reproduction of its individuals and via transferring the determinants of adaptive phenotypes to the next generations. Whatever happens in a population and influences breeding is relevant for the adaptiveness of a population. A basic assumption of evolutionary theory and life history theory is that 'animals are designed for breeding' (Stearns, 1976, 2000). This, therefore, must provide the conceptual frame in which management and husbandry of wild animals in zoos are executed (see Kaumanns *et al.*, 2020).

Adaptations and traits in the reproductive system of a species are an essential part of its '*bauplan*' (body plan). The latter also includes other traits and adaptations, for example, feeding ecology and predator avoidance. Mismatches between the 'Bauplan', and, especially, its adaptations referring to the reproductive system and living conditions, can result in breeding problems that can lead to sustainability problems and low adaptiveness of the population. With the studies on the long-term development of the historical global captive population of the lion-tailed macaque, Begum *et al.*, (2021, 2022, 2023) provide an example of a captive primate population that suffered from similar management deficiencies. Over about a hundred years of existence, lion-tailed macaques were kept in (too) small groups that did not allow the establishment of the species-typical social structures, especially the female-bonded system. Overall, the productivity of the population was low: only 60% of the adult females bred at all, individual differences in reproduction were large, and infant mortality was high. The authors pointed to a probable loss of large phenotypic and genetic diversity and discussed the development of the population, its overall poor status and conservation potential with reference to management systems that did not fully consider species typical adaptations – especially the female-bonded social system, as typical for macaques. The female-bonded social system is regarded as a key trait of the species. The key traits are primary determinants of fitness in terms of breeding conditions in each environment (see Kaumanns *et al.*, 2020).

Conclusions

The currently used approaches in the work in zoos primarily refer to essential aspects of the biology of the captive animals. However, our study reveals that Hediger's individual-based

contributions to 'Zoo biology', as well as concepts of (small) population management and of enrichment, do not fully support each other, and do not have components that facilitate their integration. This is proposed to be due to a lack of consideration of the underlying concepts of evolutionary theory and the resulting consequences for management and husbandry.

Firstly, a management plan for a population should consider and optimise the status of the individual members and their breeding units (Kaumanns & Singh, 2015; Kaumanns *et al.*, 2020). Population management should not be realised without an integrated management of its individual members and especially their breeding performance. The total of the individual members of a population constitutes the breeding potential of the population. Management and husbandry of individuals must be oriented at the 'Bauplan' and at individual-specific (acquired) traits. An essential part would be the preservation of behavioural competence (*sensu* Seidensticker & Doherty, 1996). 'Behavioural competence' refers to the various behavioural skills essential for survival and reproduction, for example, food searching, foraging, locomotion, predator avoidance, inter- and intraspecific social interactions, mating, and infant rearing. The skills and experience of a primate female in the context of infant rearing 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. To manage a phenotype, the status of the genotypes needs to be assessed and considered with special importance regarding a captive population's long-term persistence and function as a reserve. Since the establishment of breeding programmes, it has been propagated to preserve genetic diversity as a key goal (see Ballou *et al.*, 2010). Contrary to the approach as propagated traditionally by mainly using demographic management with reference to genetic aspects (see Ballou *et al.*, 2010), we propose achieving diversity by supporting species' typical life-history patterns as much as possible. The reproductive system should be allowed to function in a species-typical pattern. The study by Penfold *et al.*, (2014) indicates that management of population size and thus reproduction in a population predominantly via birth control and other 'artificial' means can reduce the reproductive potential of a population. In the lion-tailed macaque captive population, for instance, the reproductive biology of the species was ignored by, *e.g.* transferring individual females to non-natal groups for genetic reasons (see Begum *et al.*, 2023). In the wild, females remain in their natal groups throughout their lives (Kumar, 1987) and only the males disperse (Kumar *et al.*, 2001). The study by Begum *et al.*, (2023) revealed that most zoos in the global historical captive population kept lion-tailed macaques in groups that deviated demographically from those typical in the wild. The majority of the captive groups were too small, had less than five members, few adult females, and did not cover several generations. Many males were removed at a (too) young age as juveniles, and adult male tenures were long. Groups in wild contiguous forests typically consist of 16-21 individuals, usually with one adult male (with short tenure), several adult females and immature animals (*e.g.*, Kumar, 1987; Kumara & Singh, 2004; Kumara *et al.*, 2014; Singh, 2019). Groups comprise members of varying age-sex classes and generations, allowing socialisation conditions relevant for the development of species-typical behavioural patterns (see Kaumanns *et al.*, 2006). The core of the group is constituted by clans of related females that have individualised permanent relationships and strong bonds with each other (see Kumar, 1987; Thierry *et al.*, 2004; Singh, 2019).

A realisation of the concepts elaborated above and their integration in the design of future zoos would require reconsidering some of the basic goals and approaches of the current work in zoos. This especially matters with regard to the

conservation of nature and to the establishment of captive populations in zoos as reserves. Evidently, a stronger focus on the individuals of a population must consider the large differences between species and must identify what an adaptive phenotype in a given population under given living conditions should look like. A key message of our study is that management programmes should consider that the management of genetic aspects, behavioural aspects, and physiological aspects are regarded on the same level of importance.

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CONFLICT OF INTEREST

Werner Kaumanns & Mewa Singh hold editorial positions at the Journal of Wildlife Science. However, they did not participate in the peer review process of this article except as authors. The authors declare no other conflict of interest.

DATA AVAILABILITY

No additional data was used in this research.

AUTHOR CONTRIBUTIONS

WK and NB conceptualised the idea and wrote the initial draft; NB and MS reviewed the draft and assisted in preparing the final version. All authors have read and approved the final manuscript.

References

- Anderson, U. S., Kelling, A. S. & Maple, T. L. (2008). Twenty-five years of zoo biology: A publication analysis. *Zoo Biology*, 27(6), 444-457. <https://doi.org/10.1002/zoo.20177>
- Bacon, H. (2018). Behaviour-based husbandry—A holistic approach to the management of abnormal repetitive behaviors. *Animals (Basel)*, 8(7), 103. <https://doi.org/10.3390/ani8070103>
- Ballou, J. D., Lees, C., Faust, L. J., Long, S., Lynch, C., Lackey, L. B. & Foote, T. J. (2010). Demographic and genetic management of captive populations. In: Kleiman, D. G., Thompson, K. & Baer C. K. (eds.), *Wild mammals in captivity: Principles and techniques for zoo management*. University of Chicago Press. pp.219-252.
- Begum, N., Kaumanns, W., Sliwa, A. & Singh, M. (2021). The captive population of the lion-tailed macaque *Macaca silenus*. The future of an endangered primate under human care. *Journal of Threatened Taxa*, 13(9), 19352-19357. <https://doi.org/10.11609/jott.7521.13.9.19352-19357>
- Begum, N., Kaumanns, W., Singh, M. & Hofer, H. (2022). A hundred years in zoos: History and development of the captive population of the lion-tailed macaque *Macaca silenus*. Long term persistence for conservation? *Primate Conservation*, 36, 155-172. http://www.primate-sg.org/storage/pdf/PC36_Begum_et_al_100_years_captive_lion-tail_macaques.pdf
- Begum, N., Kaumanns, W., Hofer, H. & Singh, M. (2023). A hundred years in zoos II: Patterns of reproduction in the global historical captive population of the lion-tailed macaque *Macaca silenus*. *Primate Conservation*, 37, 134-154. http://www.primate-sg.org/storage/pdf/PC37_Begum_et_al_Lion-tailed_macaque_II_breeding_captivity.pdf
- Binding, S., Farmer, H., Krusin, L. & Cronin, K. (2020). Status of animal welfare research in zoos and aquariums: Where are we, where to next? *Journal of Zoo and Aquarium Research*, 8(3), 166-174. <https://doi.org/10.19227/jzar.v8i3.505>
- Caughley, G. (1994). Directions in conservation biology. *Journal*

of Animal Ecology, 63, 215–244. <https://doi.org/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(1), 78–4. <https://doi.org/10.1002/zoo.21471>

Chrulaw, M. (2020). Reconstructing the worlds of wildlife: Uexküll, Hediger, and beyond. *Biosemiotics*, 13, 137–149. <https://doi.org/10.1007/s12304-020-09376-x>

Crandall, L. S. (1964). *The management of wild mammals in captivity*. University of Chicago Press.

Erwin, J., Maple, T. L. & Mitchell, G. (eds.), (1979). *Captivity and behavior: Primates in breeding colonies, laboratories and zoos*. Van Nostrand Reinhold.

Gray, J. (2017). *Zoo ethics: The challenges of compassionate conservation*. Commonwealth Scientific and Industrial Research Organisation Publishing.

Hancocks, D. (1980). Bringing nature into the zoo: Inexpensive solutions for zoo environments. *International Journal for the Study of Animal Problems*, 1(3), 170–177.

Hediger, H. (1942). *Wildtiere in Gefangenschaft: Ein Grundriss der Tiergartenbiologie*. Verlag Benno Schwabe. (German - original German language edition that preceded the 1950 English translation).

Hediger, H. (1950). *Wild animals in captivity. An outline of the biology of zoological gardens* (G. Sircom, Trans.). Butterworths Scientific Publications. (Original work published 1942). <https://doi.org/10.1016/C2013-0-08196-0>

Hediger, H. (1954). *Skizzen zu einer Tierpsychologie in Zoo und Zirkus*. Büchergilde Gutenberg. (German).

Hediger, H. (1961). *Beobachtungen zur Tierpsychologie im Zoo und im Zirkus*. Verlag Friedrich Reinhardt.

Hediger, H. (1965). *Mensch und Tier im Zoo. Tiergarten-Biologie*. Albert Müller Verlag.

Hediger, H. (1968). *The psychology and behaviour of animals in zoos and circuses* (G. Sircom, Trans.). Dover Publications. (Original work published 1954).

Hediger, H. (1969). *Man and animal in the zoo. Zoo biology* (G. Vevers & W. Reade, Trans.). Delacorte Press. (Original work published 1965).

Hediger, H. (1982). Zoo biology: Retrospect and prospect. *Zoo biology*, 1(2), 85–88. <https://doi.org/10.1002/zoo.1430010202>

Hediger, H. (1984). *Tiere verstehen. Erkenntnisse eines Tierpsychologen*. Kindler Verlag GmbH.

Hendry, A. P., Kinnison, M. T., Heino, M., Day, T., Smith, T. B., Fitt, G., Bergstrom, C. T., Oakeshott, J., Jørgensen, P. S. et al. (2011). Evolutionary principles and their practical application. *Evolutionary Applications*, 4(2), 159–183. <https://doi.org/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. <https://doi.org/10.1016/j.anireprosci.2004.05.015>

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

Hodges, J. K., Kaumanns, W. & Gansloßer, U. (1995). Zoobiology: A scientific basis for animal management and conservation. In: Gansloßer, U., Hodges, J. K. & Kaumanns, W. (eds.), *Research and captive propagation*, Filander Verlag. pp.7–9.

Hutchins, M., Hancocks, D. & Crockett, C. (1984). Natural solutions to the behavioral problems of captive animals. *Der Zoologische Garten*, 54, 28–42.

Kaufman, A. B., Bashaw, M. J., & Maple, T. L. (eds.), (2019). *Scientific foundations of zoos and aquariums: Their role in conservation and research*. Cambridge University Press. <https://doi.org/10.1017/9781108183147>

Kaumanns, W., Krebs, E. & Singh, M. (2006). An endangered species in captivity: husbandry and management of the lion-tailed macaque (*Macaca silenus*). *MyScience* 1(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(14), 4825–4839. <https://doi.org/10.11609/JoTT.o3625.4825-39>

Kaumanns, W. & Singh, M. (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., Begum, N. & Hofer, H. (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>

Kleiman, D. G., Allen, M. E., Thompson, K. V., Lumpkin, S. & Harris, H. (eds.), (1996). *Wild mammals in captivity: Principles and techniques for zoo management*. University of Chicago Press.

Kleiman, D. G., Thompson, K. V. & Baer, C. K. (eds.), (2010). *Wild mammals in captivity: Principles and techniques for zoo management* (2nd ed.). University of Chicago Press. <https://doi.org/10.7208/chicago/9780226440118.001.0001>

Kumar, A. (1987). *The ecology and population dynamics of the lion-tailed macaque (Macaca silenus) in south India*. PhD Thesis, University of Cambridge.

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.

Kumara, H. N. & Singh, M. (2004). Distribution and abundance of primates in rainforests of the Western Ghats, Karnataka, India and the conservation of *Macaca silenus*. *International Journal of Primatology*, 25(5), 1001–1018. <https://doi.org/10.1023/B:IJOP.0000043348.06255.7f>

Kumara, H. N., Sasi, R., Suganthasakthivel, R., Singh, M., Sushma, H. S., Ramachandran, K. K. & 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(5), 976–989. <https://doi.org/10.1007/s10764-014-9776-2>

Kummer, H. (1971). *Primate societies: Group techniques of ecological adaptation*. Routledge. <https://doi.org/10.4324/9781315127415>

Lacy, R. C. (2013). Achieving true sustainability of zoo populations. *Zoo Biology*, 32(1), 19–26. <https://doi.org/10.1002/zoo.21029>

Lees, C. M. & Wilcken, J. (2009). Sustaining the Ark: The challenges faced by zoos in maintaining viable populations. *International Zoo Yearbook*, 43(1), 6–18. <https://doi.org/10.1111/j.1748-1090.2008.00066.x>

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

Lindburg, D. (2008). Reflections on the science of zoo biology. *Zoo Biology*, 27(6), 436–443. <https://doi.org/10.1002/zoo.20217>

- Long, S., Dorsey, C. & Boyle, P. (2011). Status of Association of Zoos and Aquariums cooperatively managed populations. *World Association of Zoos and Aquariums Magazine*, 12, 15–18.
- 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(2), 87–93. <https://doi.org/10.19227/jzarv7i2.382>
- Maple, T. L. (2007). Toward a science of welfare for animals in the zoo. *Journal of Applied Animal Welfare Science*, 10(1), 63–70. <https://doi.org/10.1080/10888700701277659>
- Maple, T. L. & Perdue, B. M. (2013). Zoo animal welfare. *Springer*. <https://doi.org/10.1007/978-3-642-35955-2>
- Markowitz, H. (1979). Environmental enrichment and behavioral engineering for captive primates. In: J. Erwin, T. M. & Mitchell, G. (eds.), *Captivity and behavior: Primates in breeding colonies, laboratories and zoos*, Van Nostrand Reinhold. pp. 217–238.
- Markowitz, H. (1982). *Behavioral enrichment in the zoo*. Van Nostrand Reinhold.
- 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(1), 36–44. <https://doi.org/10.1002/zoo.21469>
- Melfi, V. A. (2009). There are big gaps in our knowledge, and thus approach, to zoo animal welfare: A case for evidence-based zoo animal management. *Zoo Biology*, 28(6), 574–588. <https://doi.org/10.1002/zoo.20288>
- Mellen, J. & MacPhee, M. S. (2001). Philosophy of environmental enrichment: Past, present, and future. *Zoo Biology*, 20(3), 211–226. <https://doi.org/10.1002/zoo.1021>
- Novak, M. A., Meyer, J. S., Lutz, C. & Tiefenbacher, S. (2006). Deprived environments: Developmental insights from primatology. In: Mason G. & Rushen, J. (eds.), *Stereotypic animal behavior: Fundamentals and applications to welfare*, CAB International. pp.153–189. <https://doi.org/10.1079/9780851990040.0153>
- 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(1), 20–28. <https://doi.org/10.1002/zoo.21104>
- Poole, T. B. (1992). The nature and evolution of behavioural needs in mammals. *Animal Welfare*, 1(3), 203–220. <https://doi.org/10.1017/S0962728600015013>
- Powell, D. M. & Watters, J. V. (2017). The evolution of the animal welfare movement in U.S. zoos and aquariums. *Der Zoologische Garten*, 86(1–6), 219–234. <https://doi.org/10.1016/j.zoolgart.2017.04.007>
- Powell, D. M., Dorsey, C. L. & Faust, L. J. (2019a). 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>
- Powell, D. M., Faust, L. J. & Dorsey, C. L. (eds.), (2019b). The science of population sustainability in zoos and aquariums. *Zoo Biology*, 38(1). <https://doi.org/10.1002/zoo.21421>
- Ricklefs, R. E. (1991). Structures and transformations of life histories. *Functional Ecology*, 5(2) 174–183. <https://doi.org/10.2307/2389255>
- Schulte-Hostedde, A. I. & Mastromonaco, G. F. (2015). Integrating evolution in the management of captive zoo populations. *Evolutionary Applications*, 8(5), 413–422. <https://doi.org/10.1111/eva.12258>
- Seidensticker, J. & Forthman, D. L. (1998). Evolution, ecology, and enrichment: Basic considerations for wild animals in zoos. In: D. J. Shepherdson, J. D. Mellen, & M. Hutchins (eds.), *Second nature: Environmental enrichment for captive animals*, Smithsonian Institution Press. pp.15–29.
- Seidensticker, J. & Doherty, J. G. (1996). Integrating animal behavior and exhibit design. In: D. G. Kleiman, M. E. Allen, K. V. Thompson, S. Lumpkin, & H. Harris (eds.), *Wild mammals in captivity: Principles and techniques*, University of Chicago Press. pp.180–190.
- Shepherdson, D. J. (1998). Tracing the path of environmental enrichment in zoos. In: Shepherdson, D. J., Mellen, J. D. & Hutchins, M. (eds.), *Second nature: Environmental enrichment for captive animals*, Smithsonian Institution Press. pp.1–12.
- 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(6), 613–629. <https://doi.org/10.1007/s10764-019-00122-w>
- Skinner, B. F. (1948). 'Superstition' in the pigeon. *Journal of Experimental Psychology*, 38(2), 168–172. <https://psycnet.apa.org/doi/10.1037/h0055873>
- Skinner, B. F. (1974). *About behaviorism*. Alfred A. Knopf.
- Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *The Quarterly Review of Biology*, 51(1), 3–47. <https://doi.org/10.1086/409052>
- Stearns, S. C. (2000). Life history evolution: Successes, limitations, and prospects. *Naturwissenschaften*, 87, 476–486. <https://doi.org/10.1007/s001140050763>
- Thierry, B., Singh, M. & Kaumanns, W. (2004). *Macaque societies: A model for the study of social organization*. Cambridge University Press.
- von Uexküll, J. (1920). *Theoretische Biologie*. Berlin: Verlag von Gebrüder Paetel. (German – first edition of 'Theoretical Biology').
- von Uexküll, J. (1926). *Theoretical Biology*. In: Mackinnon, D. L., D.Sc. Harcourt, Brace & Company. Original work published 1920.
- von Uexküll, J., & Kriszat, G. (1934). *Streifzüge durch die Umwelten von Tieren und Menschen: Ein Bilderbuch unsichtbarer Welten*. Springer. (German – companion 'Umwelt' picture book).
- von Uexküll, J. (1957). A stroll through the world of animals and men: A picture book of invisible worlds. In: Schiller, C. H. (eds.), *Instinctive behavior: The development of a modern concept*. International Universities Press. Original work published 1934. pp.5–80.
- 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(1), 47–54. <https://doi.org/10.1111/j.1755-263X.2010.00142.x>
- Watters, J. V., Lema, S. C. & Nevitt, G. A. (2003). Phenotype management: A new approach to habitat restoration. *Biological Conservation*, 112(3), 435–445. [https://doi.org/10.1016/S0006-3207\(02\)00343-9](https://doi.org/10.1016/S0006-3207(02)00343-9)
- Watters, J. V., Bremner-Harrison, S. & Powell, D. M. (2017). Phenotype management: An inclusive framework for supporting individual's contributions to conservation populations. In: Vonk, J., Weiss, A. & Kuczaj, S. A. (eds.), *Personality in nonhuman animals*. Springer. pp.277–294. https://doi.org/10.1007/978-3-319-59300-5_14
- Watson, J. B. (1928). *The ways of behaviorism*. Harper & Brothers Publishing.
- Wemmer, C., Rodden, M. & Pickett, C. (1997). Publication trends in zoo biology: A brief analysis of the first 15 years. *Zoo Biology*, 16(1), 3–8. [https://doi.org/10.1002/\(SICI\)1098-2361\(1997\)16:1%3C3::AID-ZOO2%3E3.0.CO;2-E](https://doi.org/10.1002/(SICI)1098-2361(1997)16:1%3C3::AID-ZOO2%3E3.0.CO;2-E)
- Young, R. J. (2003). *Environmental enrichment for captive animals*. UFAW Animal Welfare Series. Blackwell Science. <https://doi.org/10.1002/9780470751046>