

Review

The Concept of Agency, Animal Wellbeing, and the Practical Realities of Ex Situ Breeding Programs in Zoos and Aquariums

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Abstract: Conservation and animal wellbeing are two key goals of the modern zoo and aquarium. In the case of ex situ conservation breeding programs, there is a unique paradox between these concepts; on some occasions, facilities must balance and mitigate arising conflicts between the wellbeing of animals with the goals of the conservation project. Exerting control over the reproductive lives of animals—choosing when and where they breed, whom they breed with, whether breeding is prohibited altogether, and so on—results in an inherent reduction in the animal's agency. Considering the growing recognition that providing choice and control to animals enhances wellbeing, it is essential to examine how populations and their breeding are managed. The present review presents challenges in supporting agency for animals bred ex situ by thoroughly exploring the practical realities of working with these animals. Various challenges and areas of consideration, including current research directions, suggestions for future practices, and opportunities moving forward, are highlighted. The importance of careful population management in maximising wellbeing, including the inherent dichotomy of the necessity to limit some reproductive autonomy to preserve animal wellbeing while meeting the needs of breeding programs.

Keywords: animal management; zoos and aquariums; reproduction; animal welfare; animal ethics; population management; conservation breeding; agency



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1. Introduction

Two primary goals of zoos and aquariums are conservation and upholding and maintaining the highest levels of animal wellbeing. These core goals are incorporated within all practices and processes, including how animals are managed and cared for as part of conservation breeding programs. For many endangered species of zoo-housed wild animals, carefully managed breeding programs are an essential element of the conservation work at these facilities. This work often spans multiple facilities and potentially across various countries or continents. While many zoos involved in such programs aim to maintain the genetic integrity of the captive-held population, some programs are actively involved in or working towards reintroducing endangered or extinct in the wild species into regions where they had previously been extirpated (*Partula* snails *Partula* spp.: [1]; black-footed ferret *Mustela nigripes*: [2]; scimitar-horned oryx *Oryx dammah*: [3]). Breeding programs are typically managed by a Species Survival Plan (SSP), European Association of Zoos and Aquariums (EAZA) ex situ programs (EEP), studbooks, or other similar official bodies and organisations depending on the accrediting organisation in the region and the species in question. These organisations are responsible for monitoring where individuals in the program are housed, genetic trees, and any health or other wellbeing concerns. This information is utilised when deciding which animals receive breeding recommendations and those which should not breed.

Studbooks and other programs are often required to be managed and run by individuals working in zoos and aquariums. Individuals who may manage such programs range from curators and managers to senior caregivers and research staff, to, in some

cases, full-time teams whose jobs are solely to manage and oversee the program. The program's quality can thus vary depending on the workload of the manager and other staff, the number of individuals included in the program, the topics, indicators, focus, and lens of the project, and many other factors. Some species have less rigorous monitoring, while others are intensively and holistically managed. Consequently, there are varying levels of success between managed breeding programs, with some species having very successful programs and others being less successful. Some primary concerns are a lack of fulfilled recommendations or many pairs that do not successfully reproduce despite efforts to relocate and bring pairs together for breeding [4].

The wellbeing of animals involved in conservation breeding programs is critical. The ethical and moral duty of those who work with animals under their care is to strive for excellence in animal care and predominantly positive wellbeing as outlined in the World Association of Zoos and Aquariums's strategy, *Caring for Wildlife*. For animals that are recommended to breed, better wellbeing is known to improve reproductive success on several variables, including fecundity, fertility, and survival rates of young [5]. Choice, control, and complexity in the environments of animals are essential to optimal wellbeing in front and back-of-house at all stages of life [6,7]. Providing choices empowers animals to meet their needs [8] confidently. As such, supporting an animal's agency in as many aspects of their care as possible is imperative, providing animals with choices of when, where, and how they want to do things and with whom.

A holistic animal wellbeing program includes access to appropriate nutrition, experiencing positive emotions, reducing negative emotions, and performing species-typical behaviours [6,9]. One element of many modern models of animal wellbeing is that animals should be able to live in species-typical social groups and express normal, non-harmful social behaviours. This element is at odds with some conservation breeding program activities. For example, in managing the genetics of a population by choosing an animal's breeding partner for them, the animal's ability to exert agency over mate selection and reproductive choices is inherently limited. This includes whether animals can breed in the first place, who they select as a mate, what happens to their young, and other aspects of reproduction that their wild conspecifics would have some control over.

From a sentiocentric perspective, all animals have intrinsic value and are capable of experiencing individual suffering as well as experiencing positive wellbeing. Thus, for individuals whose experiences matter from a moral point standpoint, tightly managed conservation breeding programs could be perceived as counter to the rights of individual animals. These perspectives consider that the rights of animals to bodily autonomy exist regardless of whether legal conjecture believes them to be sentient. Such perspectives might consider that in choosing when and with whom an animal reproduces, the intrinsic right to bodily autonomy is taken away [10]. Such perspectives raise an ethical dilemma for zoos and aquariums to consider. The goal of maintaining genetically viable populations of endangered species in facilities where they are safe from the pressures facing their wild conspecifics is indeed noble, but this should not come at the expense of optimal wellbeing for those animals. Therefore, a challenge is inherent to managing such programs and how zoos and aquariums can promote optimal wellbeing across all life stages, including reproduction. Wellbeing may be compromised at any stage of reproduction, and where conflicts to positive wellbeing may arise, steps to mitigate negative stressors and other potential unfavourable welfare challenges must be in place.

In the present review, current challenges and opportunities in supporting the agency of animals who are part of conservation breeding programs are presented through a thorough exploration of the practical realities of working with animals who are involved in studbooks or other managed breeding programs. Highlighting, acknowledging, and exploring these challenges and areas of consideration, including current directions in reproductive agency research and suggestions for future practices and opportunities, are illustrated.

2. Reproductive Choice

A key choice surrounding the reproductive lives of animals is whether they breed at all. Many species experience seasonal reproductive cycles wherein they are behaviourally motivated to breed. From the perspective of some and following many contemporary welfare models, including the Five Domains model [9], this would, in theory, come under an animal's right to display species-specific natural behaviours including social and breeding behaviours. In some species, sexual activity may not only be for reproduction but can be a method of maintaining social bonds or for pleasure (bonobos *Pan paniscus* [11]; bottlenose dolphins *Tursiops truncatus* spp. [12]). However, for many reasons, an animal might not be permitted to breed or engage in sexual behaviours to safeguard the animal's welfare. For example, the animal may be a carrier of a hereditary disease, such as hip dysplasia in big cats and canids, or the animal may be over-represented in the gene pool of the existing population. There is one argument that animals should be allowed to breed freely and whenever they choose; however, it is also essential to consider the wellbeing of any young animals and their future. In the case of hereditary disease, it is better not to allow such genetic conditions to proliferate in the population and thus prevent poor health and other welfare outcomes in the future.

Reproductive management programs for conserving endangered species involve some level of human control over the different stages of natural breeding. This includes human intervention in selecting mates, when and where they mate, how they rear their offspring, and so on. Of course, while an argument can be made that animals should be able to exert their own choices about their reproductive lives, it is essential to consider the implications of allowing free reproduction. Animals in the wild and, indeed, in human care may not necessarily make optimal choices for their wellbeing or the wellbeing of their young. They may reproduce too young or not in the right circumstances simply because it is their instinct to do so. For animals where the male coercively or forcefully mates with the females, the female may not have a choice to begin with [13].

Furthermore, an animal's selection of mates may not be optimal for the genetic health of their young, or they may choose to neglect or improperly rear their young after they are born. The opportunity to breed is thus not necessarily in the mother's or her young's best interest from a wellbeing perspective. A study on chimpanzees (*Pan troglodytes*) living in human care found that the opportunity to reproduce and rear young was not associated with positive indicators of welfare, challenging the popular assumption that the chance to reproduce is intrinsically beneficial to the wellbeing of the potential mother [14]. Human caregivers can look ahead and understand more holistically the potential impacts of reproduction on the wellbeing of an individual animal and a larger social group. This includes reviewing all available information the animals would likely need to consider when making reproductive choices. Human caregivers can make an informed decision based on science, ethics, and empathy for the animals. Consequently, reproductive control is often the most appropriate course of action to ensure that when animals reproduce, it is under the circumstances and in care that supports positive wellbeing for the mother and young.

Various forms of contraception are utilised by those managing individuals or populations of breeding animals. The aims of contraception are variable: to manage the population's genetic composition, reduce inbreeding, and modify generation length as the primary concerns [15]. Different forms of contraception may also be considered for goals such as modifying undesirable social behaviour, such as testosterone-related aggression (antelopes [16]; elephants [17]; primates: [18]), for the therapeutic management of reproductive system health (canids [19]), and in overall improvement of animal wellbeing by allowing the maintenance of social groups and reducing the physiological demands of pregnancy and rearing offspring [14]. The effectiveness of different contraceptive methods is considered when discussing which methods are appropriate for limiting reproduction in zoo-housed animals. However, there is much evidence of zoos' successful implementation of various methods [20–22]. The effectiveness of different methodologies and procedures

at limiting reproduction is not the focus of this paper; instead, the discussion is geared towards the impact of different strategies on animal wellbeing in consideration of their agency and psychological wellbeing. For more in-depth reviews on the effectiveness of the many different methodologies available, see Agnew and Cheyne [20] for a review of reproductive control methods in primates, Patton et al. [21] for a review of ungulates, and Asa and Moresco [22] for a more general overview for wildlife species.

3. Mate Choice

One of the most essential components of reproductive behaviour in many sexually reproducing animals is how they select partners. This includes all elements of mating behaviour, including the sex which is most important in mate choice, how many individuals an animal mates with, how often they mate, and how an animal chooses their reproductive partners. The reproductive strategy of an animal varies depending on the species; for example, in some animals, the female chooses or rejects the males (striped-faced dunnarts *Sminthopsis macroura* [23]), [24] while in others, males select the females [25] sometimes using coercive strategies [13]. Some species live in family groups with one breeding pair (canids [26]), while other species may live in multi-male or multi-female harems (ungulates [27]; primates [28]). In the wild, individuals of many social species will disperse from their natal group to find and select a mate in a different group or live a solitary life where their territory may overlap with those of potential mates [29]. Naturally, when animals live in human-managed environments, it is not always possible for them to make this choice themselves. Instead, they may be transferred to another social group housed elsewhere according to their caregivers' decisions or the needs of the population management plan.

Translocations are known to be stressful experiences for animals. Animals that have recently experienced transport often experience increased physiological stress and other indicators of compromised wellbeing such as behavioural changes [30,31]. The process of translocation exerts multiple negative stressors, including capture and restraint for transport if animals are not trained to participate voluntarily, confinement during the transport process, which may be by land, sea, or air, and eventual release in an unfamiliar environment, to unfamiliar animals and unfamiliar care staff. There are processes in place for accredited zoos to ensure that transfers are not unnecessarily carried out, such as those from the British and Irish Association of Zoos and Aquariums (BIAZA) and the American Association of Zoos and Aquariums (AZA), and to facilitate the smoothest transition. Of course, transferring one or both individuals in a breeding pair may be unavoidable for ex situ breeding programs. Many wild species do not have successful or well-studied methods for artificial insemination [32] which means animals must be brought together for breeding in most cases. Due to the inherent population size constraints associated with housing animals in zoos and the logistical, financial, and practical challenges related to translocations, many healthy, fertile animals may never reproduce, even for highly endangered species [33]. Some studbooks consider aspects such as distance of transport and the impact of transfers on wellbeing, sometimes choosing to transfer animals to breed with a less preferable but still good match at a closer distance than with an individual further away. While more widespread adoption of assistive reproductive technologies (ARTs) would aid in mitigating the need for transfers, ARTs are not widely available nor studied for many endangered species that are part of ex situ conservation breeding programs [32,34]. This means that zoos often rely on bringing animals physically together, in some cases from the other side of the world, hoping the pairing will succeed and result in young without intervention.

There are wellbeing implications for transferring animals to new social groups and unfamiliar environments. The social life of different species of animal varies from predominantly solitary animals which raise their own young (tigers *Panthera tigris* [35]), small family groups (gorillas *Gorilla gorilla* [36–38]), fission–fusion (spider monkeys *Ateles* spp. [39], dolphins [40]), stable long-term social groups (elephants [41]), and all manner of other social styles. Depending on the social style of the species and individual factors such as age,

sex, temperament, and previous experiences, disrupting the social life of the individual or group of animals can be quite significant [42,43]. This effect may extend to scenarios where animals are transferred without familiar and bonded conspecifics. Transporting animals with animals with whom they are already familiar, such as family members and those with whom they have strong social bonds, may be beneficial as a buffer against the stress of translocation. Potential recommendations include allowing animals to transfer alongside members of their social group. However, this is an uncommon requirement for translocations and is often only considered on an informal, not systemic, basis. There is presently a gap in the literature addressing the impacts of translocations on zoo animals that specifically addresses how changing social groups as well as changing caregivers impact the wellbeing of animals, and while this is an understudied topic, a lack of scientific basis should not preclude attention to these factors from consideration.

Moreover, introducing animals for any purpose, including breeding, is risky. There is no guarantee that animals will be compatible beyond genetics, and there is always a risk of injury and even death during introductions. There is no guarantee a newcomer will be accepted into the social group. While this choice is ultimately down to the animals involved, it is not ideal to subject an animal to the stress of translocation for them to be rejected by a new social group. Of course, there is very little zoos can do to predict the risk of adverse outcomes when introducing animals for breeding. Personality has been suggested as one method of determining group compatibility [44]; however, there is a need for more evidence to implement personality effectively as a tool for predicting outcomes of transfers or whether a pairing is likely to be successful. Ultimately, a thorough risk assessment will always be necessary to determine whether the conservation benefit of bringing animals together for breeding outweighs the potential short and long-term risks to wellbeing.

Providing Mate Choice

Providing animals with choices as a component of selecting breeding pairs may be a valuable tool for improving the success of program goals. In particular, allowing animals with choices over potential mates can increase the success of pairs while improving upon animal wellbeing. In free-living contexts, animals are expected to make mate choices that maximise their breeding success, such as choosing mates who are healthy, genetically distant from themselves, and socially compatible [45]. Understanding the mechanisms underlying mate selection behaviour and how animals make mate choices is essential to simulating mate choices in captivity that reflect the decisions animals would likely make for themselves. Free mate choice, defined as allowing animals to select their mate from a pool of multiple mate choices, is one such method of simulating mate choice in human-managed contexts. Free mate choice has proven benefits for breeding programs for several species. For example, giant pandas (*Ailuropoda melanoleuca*) who were allowed to choose their mates freely had improved reproductive success, and this effect was increased when the choice was mutual between both members of the pairing [46]. Various zoos have experimented with showing videos of potential mates to female great apes to see which male was looked at the longest and with the most interest and then bring over this male.

There are, of course, challenges associated with providing animals with a free mate choice. Firstly, it is neither feasible nor conducive to animal welfare to transport all potential mates to one site for the animals to choose from. Secondly, allowing animals to freely mate with whomever they choose may not be in the best interests of the whole population's genetic health. Thirdly, introducing animals—even if only to see if they are compatible briefly—can be stressful and pose potential health and safety risks to all animals involved, as discussed earlier. To mitigate these challenges, scent has been proposed to allow animals to indicate mate preference before introducing a pair for breeding. In practical experiments using this method several species, including stripe-faced dunnart [23], cheetah [47], and harvest mouse (*Micromys minutus* [48]), experienced greater pair and reproductive success when paired with the males they demonstrated a scent preference for. It is, therefore,

possible to use easily transportable substances such as samples of urine or faeces for tests of scent preference and eliminate the need to move any animals long distances or use technology such as screens and displays to allow animals to select from possible mate choices. As an example, Mosotti et al. transported urine samples from males for female cheetahs to choose from. The females reliably demonstrated a scent preference for males most genetically distant from themselves [47]. Furthermore, in their study of stripe-faced dunnarts, Parrott et al. [23] demonstrated that freezing scent samples for up to 40 days did not impact scent preference in females, indicating that such methods may be broadly useful even for potential pairs who live significant distances apart.

By understanding the mechanisms underpinning mate choice through experiments of scent preference and free mate choice, it may be possible to predict likely mate choices for animals based on genetic distance and individual animal personalities [49]. Seyfarth et al. suggest that personality might be linked to certain social measures critical to reproductive success [50], while Powell and Gartner suggest that personality may have a role in mate selection [51]. Similar personality has been suggested as a predictor for reproductive success in species including black rhinoceros [5] and giant pandas [46], and personality traits such as sociality have been found to influence reproductive frequency in species such as cheetah [52,53]. Breeding programs could utilise more exhaustive personality databases to retrospectively study the factors influencing the reproductive success of pairings and make more informed choices in the future [44]. While such research is still in the early stages, personality nonetheless presents a promising future direction for conservation breeding programs that consider the likely preferences of the animals themselves.

4. Training and Handling

Animals who are managed ex situ for breeding programs are often subject to regular veterinary procedures to monitor reproductive health and collect valuable data for research on reproductive physiology. Ultrasound scans and sample collection are typical procedures [32,54]. Health checks are essential to monitoring holistic animal wellbeing and should include all aspects of animal care, including the inputs given to animals by their caregivers. This includes their environment, diet, enrichment, human–animal interactions, and other care elements, as well as the outputs displayed by the animal, such as hormonal levels, physical fitness, behaviour, social interactions, and other indicators. While some elements of these wellbeing checks can be conducted non-invasively, such as behavioural monitoring, many essential procedures require animals to be handled for the collection of samples or physical examination.

In the case of handling routine procedures, the wellbeing of animals involved in breeding programs must be considered holistically and from their perspective, including their affective states. For example, it is well known that forceful and coercive handling methods are stressful [55,56] and that chemical restraint without effective positive reinforcement training beforehand is stressful and frightening from the animal's perspective. Therefore, caregivers handling animals should focus on methods that provide animals with agency and create positive experiences. Positive reinforcement training (PRT) has been used successfully to train animals in zoos to participate in their care for a variety of procedures for many years, including crate training [57,58], blood draws [59,60], X-rays, dental care, weighing, and other procedures [61].

Animals involved in conservation breeding programs should be trained and habituated to participate in relevant procedures, such as blood draws and ultrasounds, as soon as possible. Early training ensures that when these procedures are needed, the animal already considers the experiences to be a positive and voluntary event. PRT has been used to great effect in habituating zoo-living animals to ultrasound procedures; for example, a snow leopard (*Uncia uncia*) was trained to present the abdomen for ultrasound at the barrier between the caregivers and the animal to allow ultrasound procedures to be carried out while she was awake [62]. Many good examples of training and new and innovative ideas

for training animals have been conducted in zoos worldwide and are a positive direction for many breeding programs.

5. Rearing Young

Where choices in some aspects of animals' reproductive lives may have to be taken away or limited, there are possibilities throughout the reproductive process that support animal choice and control. For example, Greggor et al. provided multiple choices of nesting sites for birds that were part of a Hawaiian bird conservation breeding program at San Diego Zoo [63]. In this study, birds were provided with various supportive infrastructures ranging in location and difficulty as nest sites, providing the animals with multiple choices for where and how they wanted to nest. Such interventions are relatively simple and can be as easy as giving different options for nesting materials, allowing animals to build their nests where they choose and with the materials they prefer [64,65].

Occasionally, animals may not be effective at parenting their young—particularly for first-time parents without prior experience. Consider cases where the young animals are abandoned or the parents are ineffective, particularly for endangered species that may infrequently reproduce. It may be the case that there is a suitable alternative parent of the same species other than the biological mother, and alloparenting may be possible. However, this is not possible in all cases, particularly when discussing solitary species. In that case, traditionally, human intervention through supplemental feeding or hand-rearing of the young has been deemed necessary. While human intervention is sometimes the best option for improving an animal's chances of survival when parenting from the animal is inadequate, other alternatives may reduce the need to interfere with the parents' agency or increase the young's dependence on human care. Best practices today include bottle or other feeding practices that briefly remove the young from the group, feeding the young while they are in the group and held by the mother or other group members, or housing the young with conspecifics next to the group to be able to feed and also maintain social contact. Young reared with human intervention should still be given opportunities to interact with, or at least be near, conspecifics instead of being isolated in another area away from the group. Removing animals from their group, isolation, or even taking animals home, which is still a common practice today, should be reconsidered in favour of modern approaches which fulfil the aforementioned requirements.

One of the other ways humans can assist with rearing is through positive reinforcement training to help improve behaviours associated with rearing youngsters, which encourages appropriate behaviours and discourages ineffective ones. For example, a bottlenose dolphin (*Tursiops truncatus*) displaying an undesirable behaviour not conducive to parenting—grabbing her calf in her mouth and dragging him—was trained with a 'no' signal to stop this behaviour [66]. Positive reinforcement training could be utilised to encourage more effective parenting in prospective parents; for example, rewarding the mother for feeding her young if she had previously been negligent with providing her young enough food.

Outcomes for Young

It is impossible in the contemporary zoo world to discuss the topic of agency in breeding programs without considering the ethical implications of allowing free breeding. Some consider free-choice breeding key to excellent and natural wellbeing, even if the young are euthanised at a weaning age. Competing approaches to animal ethics arise when animals can freely reproduce [67]. Just as zoos are responsible for the wellbeing of any breeding animals, they are also responsible for what happens to the young that result from any breeding that occurs on-site throughout the lifespan of that animal. This means considering whether they have the resources to care for the animal, including space to house the animal long-term throughout her lifespan, regardless of whether they are of genetic importance to the species management program. Culling animals that are not considered genetically valuable is already commonplace and is regarded by many facilities as a routine and normal aspect of managing breeding populations [68]. However, modern

and professional facilities should avoid relying on traditions and “what has always been done” when more compassionate and ethical approaches are available and practical. As organisations concerned with promoting positive animal wellbeing, it is arguable that, through effective population management and careful breeding of animals using well-planned whole lifespan reproductive planning and timed use of contraception, it is possible to limit the number of animals deemed surplus to requirements. There is a moral and ethical imperative to create opportunities for lifelong positive wellbeing and longevity for all animals born to managed breeding programs. Many have put forth similar ethical and moral arguments against culling surplus animals [68,69]. Indeed, the focus should not be on how to deal with already living animals deemed to be surplus, who should be cared for with respect to their wellbeing as much as any other animal, but instead on how conservation breeding programs, and zoos in general, can avoid needless reproduction that results in surplus in the first place. Inevitably, careful population management that avoids the birth of animals that might be considered surplus requires some level of limiting choices and opportunities for animals to reproduce and exhibit associated reproductive behaviours. The goal, overall, is for all animals living in human care, both present and future, to be treated with equal consideration and given the opportunity to live long, positive, and fulfilling lives.

There is also the matter of how the young that are born are managed. This can include those who may go on to reproduce themselves and how their social groups are managed in light of the likelihood of animals needing to be eventually moved or transferred to other groups. In particular, it is essential to consider when youngsters are likely to move on from their natal groups when it is known that removing young from their mothers before they are naturally ready can be detrimental to animal wellbeing [70]. Juveniles in free-living contexts may eventually disperse from their natal group to enter another group for multiple purposes; the females of some species will not reproduce again until their previous youngsters have matured and dispersed, and so some zoos may choose to move the young on to encourage the female(s) to breed again. In other cases, animals will move on to another breeding group in the hopes they will reproduce in the future. In all cases, mother-young bonds should not be broken before is appropriate based on the natural life history of the species in question. Such bonds are essential to proper psychosocial development in many species [71] and unnecessary early separation is thus detrimental to both normal development and the wellbeing of both individuals. Newberry and Swanson proposed several strategies for easing the difficulty of maternal separation in mammals, such as providing both the mother and her young with opportunities for brief periods of voluntary separation to desensitise both animals to being apart [70]. Positive reinforcement training also helps the gradual separation process, ensuring the experience is positive for both animals. Creating appropriate, challenging, and complex environments is also essential to encouraging young animals to become independent from their mothers, appropriate cognitive development, and integral to overall wellbeing.

6. Holistic Animal Wellbeing

There are fundamental ethical questions underlying many decisions surrounding individual animal wellbeing within breeding programs. For example, while translocations and introductions are stressful for animals, a positive outcome for the whole population from transferring that animal for breeding outweighs the compromise on animal wellbeing. However, suppose compromises are to be made in one aspect of the animal’s life for the so-called “greater good”. In that case, it is imperative that all other aspects of care are carefully monitored and assessed, and every effort is made to minimise the adverse welfare outcomes associated with breeding and promote positive emotions. Equipped with the knowledge that husbandry practices and management influence breeding success [72,73], promoting good wellbeing in all animals involved in conservation breeding programs is a priority to fulfil the shared goals of optimal animal wellbeing and conservation success.

As a practical example, gestating or lactating females may be held separately from the wider social group in a relatively confined breeding den to protect the mother and her youngsters from injury or disturbances from the wider social group and zoo visitors. While providing the mother with 24/7 access to all areas of the habitat is undoubtedly a preferable approach for allowing the animal to exert agency over her life and where she is choosing to be, there may, even so, be instances and individual scenarios where separation is required. In such cases, the holding areas where breeding animals are kept, and all other back-of-house areas, should be just as complex with as many behavioural opportunities as other areas of the habitat [7]. This may include providing refuges for animals to retreat if they want space away from their youngsters, nesting sites with different microclimates, areas further away from public viewing spaces, etc.

There is an area of potential future development in animal welfare science that considers the different opportunities for incorporating animal-centred technology into enclosure design. For example, Coe and Hoy describe the potential for technologies such as motion sensors that could be used to give animals control over environmental parameters such as ambient lighting, temperature, humidity, sound, and so forth, allowing animals to have more control over their environment even at times when there are no staff on-site to control these elements [74,75]. Such ideas are transferable to the management of animals involved in conservation breeding programs including their everyday management, when they are breeding, raising youngsters, and at other times in their reproductive lives. For example, how might the wellbeing of a nesting mother be improved if she were given the opportunity to control the temperature of her den? Of course, many zoos are limited in their ability to implement specific technology due to financial or other resource constraints; this does not mean opportunities to implement choice and control are unavailable. The quantity and quality of substrates and effective environmental enrichment have been highlighted as areas where improving the wellbeing of animals can be interconnected with improving the outcomes of breeding programs [76]. Enrichment, for example, can provide additional complexity in a habitat; a simple puzzle can allow animals to decide when to forage by only releasing food when the puzzle is completed [77]. Enrichment devices enabling animals to choose when and where they would like to fulfil their needs are also beneficial during overnight hours when no care staff are on-site to provide the animals with food or other resources. Nesting mothers, in this case, may be provided more opportunities to choose when they leave their den to feed that does not revolve around the schedules of their human caregivers but instead based on their own needs, wants, and preferences and how they choose to rear their youngsters.

Animals should be allowed opportunities to self-maintain and be competent in their care at all hours of the day [7,63]. To be competent means to be able to fulfil many, if not all, of their own needs in the absence of humans; this means having the ability to move freely, to clean themselves, to find food and water when they are hungry or thirsty, to rest where they want to rest, and make all manner of other choices about what they need and when they need it. Animals having the ability to self-maintain is one method of measuring psychological wellbeing and the presence of positive emotions in animals [78]. The ability to perform self-maintenance behaviours should always be supported and encouraged for animals throughout their lives, including during breeding and gestation while rearing their young and outside of breeding seasons. Continuous assessment of wellbeing holistically using animal-based indicators, such as the expression of self-maintenance behaviours and the presence or absence of undesirable behaviours [79], as well as positive interactions with other animals and staff, all can be used to great effect in providing insights into psychological wellbeing throughout every stage of conservation breeding programs and are essential in contemporary animal welfare management programs today.

While a good life is at the core of contemporary zoos and aquariums, more thought, research, and review need to go into how animals are cared for and how care decisions affect animal wellbeing. This includes looking at animal wellbeing in the short term and considering the long-term effects for the individual and the species. Holistic animal wellbe-

ing also presents challenges and allows for appropriate social, motor, and psychological development. Through being exposed to and learning how to handle a wide variety of situations and stimuli, animals build their resilience and, thus, their capacity to adapt and cope with future adversities [80]. Such considerations are essential to conservation breeding programs, wherein the ultimate goal should be to preserve populations of animals who can be resilient in the face of the challenges they may face in the wild [81]. While wellbeing should be predominantly positive, challenges can be presented through novel enrichment, complex habitat design, and opportunities to overcome challenges to receive rewards, such as through puzzles or positive reinforcement training [82]. Genetic fitness and animal welfare was one of the topics discussed in the first Population Management and Animal Welfare session included in the Joined Taxon Advisory Group (TAG) meeting in Budapest, Hungary, in 2018. The session featured speakers discussing the opportunities and challenges of considering individuals versus species [83]. This yearly meeting continues to bring together members from all significant zoo associations, and it is proposed that including an animal-wellbeing-specific session in such meetings and conferences would aid in putting animal welfare explicitly on the agenda for conservation breeding programs.

Refer to Table 1 for a checklist of areas to consider when developing holistic conservation breeding programs for wild animals living in human care. This list of areas to consider is by no means exhaustive. Still, it provides a framework upon which species management plans and individual facilities caring for animals during reproduction can build when planning, preparing for, and implementing breeding recommendations.

Table 1. A framework for planning and evaluating conservation breeding programs that incorporate animal agency ideas and holistic wellbeing into their processes.

Element	Description
Lifetime reproductive planning	The reproductive lives of animals in conservation breeding programs should be mapped out as early as possible to promote optimal reproductive health, overall wellbeing, and appropriate intervals between generations.
Timing and circumstances	Animals should reproduce only at times and in circumstances where the care and wellbeing of both the mother and her future youngsters will be optimal at all stages.
Contraceptive method(s)	Social, chemical, and surgical contraceptive methods are available, and the method chosen should be appropriate not only for the species but for the individual circumstances of the animals with respect to individual and group-level wellbeing.
Mate choice	Where possible, the selection of mates should consider not only the genetic element of reproduction but also consider distance travelled, individual circumstances, and suitability for transfer, including a consideration for the mechanisms underpinning mate choice and what the animals themselves are likely to select.
Handling and training	Positive reinforcement training methods should be incorporated into all conservation breeding programs to support essential procedures, such as ultrasounds, to be carried out efficiently, safely, and with attention to the animal's agency and ability to choose whether they want to participate. All handling and training of animals should be positive and meaningful from the perspective of the animal.
24/7 housing and husbandry	Animals should have as much choice and control as possible in all areas of their lives, reducing their dependence on human caregivers to meet their needs as much as possible. This includes consideration for all areas of the habitat, including back-of-house areas such as nesting areas, birthing dens, and so on, as well as opportunities for a wide range of species-typical and positive behaviours through the provision of dynamic habitat design and enrichment.

Table 1. Cont.

Element	Description
Careful planning of transfers	Breeding for conservation inevitably requires translocations. All translocations should be thoroughly planned to promote the smoothest transition possible, including consideration for the wellbeing implications of transferring an animal away from a familiar habitat, conspecifics, and caregivers.
Outcomes of youngsters	The outcome of a breeding recommendation should be considered and evaluated as early as possible, including when and how a youngster disperses from the natal group. Considerations should include the future of the population as a whole, including whether the goal is to release animals into the wild as an ultimate outcome and how to support a population that will be resilient to challenges faced both in human care and potentially in the wild.
24/7, across lifespan wellbeing for all animals	All steps should be taken to support providing all animals with the opportunity to live full, meaningful, and positive lives. All possible steps to reduce the number of animals considered “surplus” should be taken, with the goal of eliminating, the need to euthanise healthy individuals for population management purposes.

7. Reproductive Technologies and the Future

With the advent of the 21st century, many reproductive technologies that have become commonplace in the reproduction of domestic species are now being tried and tested with animals in zoos and aquariums [32,84]. For some species, ARTs such as artificial insemination may be the only option for viable reproduction of a species or subspecies. The northern white rhinoceros (*Ceratotherium simum cottoni*) is one example, with severely limited wild population sizes and reduced extant gene pool [85]. With only two living females each with limited reproductive lifespans, artificial insemination and surrogacy are the final options for preserving the subspecies utilising preserved somatic cells from deceased individuals [86]. Trials of artificial insemination in rhinoceros have been successful, presenting a possible option for producing viable offspring and restoring genotypes which had been lost [87]. The existence of biobanks and available germplasm from endangered and extinct-in-the-wild species thus creates opportunities to reintroduce genetic potential that does not currently exist in the extant population [88–91].

Where agency and wellbeing are concerned, the opportunities and challenges of utilising ARTs are complex. Naturally, when artificial insemination and similar ARTs are utilised, animals are denied opportunities to express natural courting and reproductive behaviours that precede reproduction. Thus, the debate about the reproductive agency of animals continues to be raised. However, ARTs still play an essential role in ex situ population management. Where the benefits to wellbeing outweigh the potential challenges, ARTs provide a valuable alternative to lengthy and stressful translocations of animals. Semen and other materials can be stored and transported over long distances [92], reducing the need to transfer animals across long distances for breeding purposes.

Furthermore, genetic material can be transferred over much longer distances than it may be logistically possible for animals. Much recent research has focused on improving the storage and transport of semen for these purposes [93]. Thus, the global potential to collaborate on ex situ breeding programs can be increased without compromising on animal wellbeing. Finally, and importantly, the risk of pairs not reproducing despite being recommended for breeding can be mitigated through the successful implementation of ARTs. The wellbeing risks associated with introducing animals to new social groups are also avoided, which can be especially prudent to consider for highly endangered species with limited population sizes and, thus, limited options for breeding pairs. The genetic material of one male can be used to inseminate multiple females, for example, without needing to transfer that male out of his current social group.

Of course, it is important to consider that testing many reproductive technologies with zoo species is difficult owing to small population sizes, an even more limited number of which are considered for breeding, and the many unique reproductive systems involved [32]. Only viable individuals—i.e., those cared for under optimal conditions for wellbeing—are to be considered in ex situ programs. Of those individuals, only a small number will be considered for potentially invasive trials of ARTs for some species, and experimentation with various technologies may not be possible under current conditions. The need for integration between ex situ and in situ population management and the expansion of technologies through research is highlighted by the International Union for the Conservation of Nature's (IUCN) One Plan Approach (OPA), and further through the lens of One Conservation [94]. These approaches emphasise improving all aspects of managing populations, including developing new technologies that safeguard animal wellbeing in the wild and human care while maintaining genetically healthy populations. Indeed, such new ventures in ARTs should be explored in greater detail where possible in pursuit of a balance between animal wellbeing and preserving the genetic potential of endangered species.

8. Conclusions

A key future shift in how breeding programs and studbooks are maintained is to encourage and facilitate consistency in running such programs and reduce or eliminate discrepancies in programme quality. All ex situ breeding programs of exotic animals should consider how providing choice and control in the reproductive lives of animals can be integrated into all processes, from selecting mates to how youngsters are handled. Thorough recordkeeping and retrospective studies of the factors that influence mate choice and successful reproduction are essential to enhancing our understanding of mate selection in ex situ breeding programs and, as such, research should be embedded into the core purpose of the programme and encouraged for all species that are part of such initiatives. By understanding the mechanisms by which animals select mates and what qualities influence the likelihood of pair success in a wide variety of managed species, caregivers and those responsible for managing breeding programs can make more informed choices about breeding recommendations and the pairings which are likely to be both successful and beneficial to the wellbeing of the animals.

Where some elements of an animal's agency must inherently be limited when managed as part of a breeding program, opportunities for choice and control in all other aspects of their lives must be available to promote optimal animal wellbeing. This can include allowing animals to make decisions about aspects of their reproductive lives, such as nest building, how their youngsters are reared, their ability to self-maintain, and so forth. Caregivers should be encouraged to take an active role in breeding programmes; as animal caregivers work with their animals daily and are the most familiar with their behaviour and preferences, they are well-equipped to inform and participate in discussions surrounding reproductive decisions concerning those animals. Good conservation breeding programs consider the whole animal beyond their genetics, including their physical, behavioural, and psychological needs. With sufficient choice, control, and attention to wellbeing, the needs of conservation breeding programs can be met while promoting a positive quality of life throughout the lifespan of mothers, fathers, youngsters, and all other animals.

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