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Review article

Solvable challenges, meaningful lives – welfare and reproduction in zoo animals

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Abstract

In the management and care of farm animals and pets, controlling reproduction is common practice to an extent that its justification is rarely questioned. In zoo population management, limited holding capacity and difficulties in culling so-called 'surplus animals' lead to a widespread use of reproductive control measures. The argument that preventing reproductive behaviour represents a welfare compromise has been put forward repeatedly in dicussions about zoo population management. However, reports on the effect of limiting reproduction on individual or whole group welfare are surprisingly sparse. Here, we focus on welfare-relevant aspects of preventing reproduction. Welfare-based decisions regarding the use and choice of reproductive control methods can only be taken if every aspect of a species' reproductive behaviour and physiology is taken into account. To ensure zoo animal welfare, we need not only protect zoo animals from distress, but need to provide a meaningful life with solvable challenges on a continuous basis. Reproductive behaviour may be considered a very appropriate challenge for an individual animal that its species evidently evolved to solve. Considering the lifetime of an individual, reproductive activity may represent a comparatively small portion of its activity budget, or a very large portion of its overall lifespan. When considering reproductive control in zoo animals, one needs to be aware of the entirety of potential positive and negative welfare effects on an individual, and of the possible need to fill the gap in life time no longer occupied by reproductive activity.

Introduction

A large body of literature documents how poor animal welfare negatively influences reproduction in farm animals (e.g., Tiezzi et al. 2019; Pol et al. 2021; da Silva et al. 2023). By contrast, how reproduction affects animal welfare has received less attention. Whereas reproduction is arguably one of the most important characteristics of animals with a very high intrinsic motivation (Kaumanns et al. 2020), it has been under human control so intensely for such a long time that its absence or only marginal occurrence in animal welfare checklists, such as the so-called Five Domains Model (Mellor et al. 2020; Miller and Chinnadurai 2023), might largely go unnoticed. The active management of reproduction, and in particular its prevention, is a prerogative of, and precondition for, many forms of animal husbandry. Actually, managing animal reproduction is such an integral part of agricultural and pet animal husbandry that its methods are taught, that health risks related to the different contraceptive strategies are known, but its potential effects on psychological animal welfare, and putative measures of mitigating these effects, are rarely mentioned. The fact that we manage animal reproduction, and thus prevent a very large number of animals from reproducing, is taken for granted, which may or may not be linked to a default perception that preventing animals from reproduction is ethically justified and does not affect their welfare (e.g., Faria 2025).

Nevertheless, intervention in natural reproductive behaviour has been identified as welfare-relevant in the scientific and philosophical literature. For example, there are pathocentric welfare concerns related to the short-term pain associated with castration (Robertson et al. 1994; Stafford and Mellor 2005; Prunier et al. 2006; Rault et al. 2011; Yun et al. 2019), health issues associated with hormonal contraception (Murnane et al. 1996; Chittick et al. 2001; Munson et al. 2002; Asa et al. 2014; Needham et al. 2017; Wang et al. 2023) or with the absence of reproduction in intact females (Hermes et al. 2006; Penfold et al. 2014; Wongsaengchang and McKeegan 2019). Additionally, the prevention of reproduction is considered as a psychological welfare constraint, because we putatively prevent animals from experiencing positive affective states associated with reproductive (sexual and parental/social) behaviours (Panksepp 2005; Englund and Cronin 2023), including their positive hormonal feedback loops involving, for example, endorphins and oxytocin. On the other hand, preventing reproduction can be seen as a welfare enhancement due to the reduction of stress, energetic demands and aggressive behaviours usually associated with mate choice competition and mating (or only the sheer motivation to reproduce) (Vaughan et al. 2014). In addition, parental care may also be considered a stressful task in different species (Klug et al. 2012; Sawecki et al. 2019; Alekseeva et al. 2020).

Considering the welfare relevance of reproductive activity, unrestricted breeding and irreversible gonadectomy (through surgical or chemical means, resulting in the reduction of reproductive hormones and behaviour) present the two extremes of reproductive control (Figure 1). A variety of methods are available in animal husbandry that curtail reproduction and reproductive behaviour to different degrees. They all have advantages and disadvantages, which may vary depending on the species or even the individual under treatment (Figure 1). For example, in a 15-year old female Asian elephant *Elephas maximus*, delaying reproduction for several years by contraception or separation of the sexes may be detrimental for her reproductive potential (Hermes et al. 2004; Bertschinger et al. 2018) and the building of her future matriline. In contrast, the same method applied to her mother, 55 years old and suffering from severe degenerative joint disease, may be critical to ensure her health status and group wide social cohesion, without needing to separate her from the social group.

No systematic treatment of these questions exists in the zoo animal literature to our knowledge. Considerations of welfare-related aspects of reproduction are particularly relevant for zoo animal management, where an optimum of welfare presents one of the defined husbandry goals (Ward et al. 2018; Miller and Chinnadurai 2023). An exhaustive literature survey is beyond the scope of this review, because of the species-specificity of reproductive behaviour. Therefore, our intention is to introduce readers to the topic, to outline certain concepts we consider significant, and thus initiate a more detailed discussion within the zoo community and the public concerned with zoo animal husbandry and welfare.

Preventing reproduction: managing animal stress and aggression

Apart from the evident aim of preventing offspring, prevention of reproduction is mostly related to the management of mate-

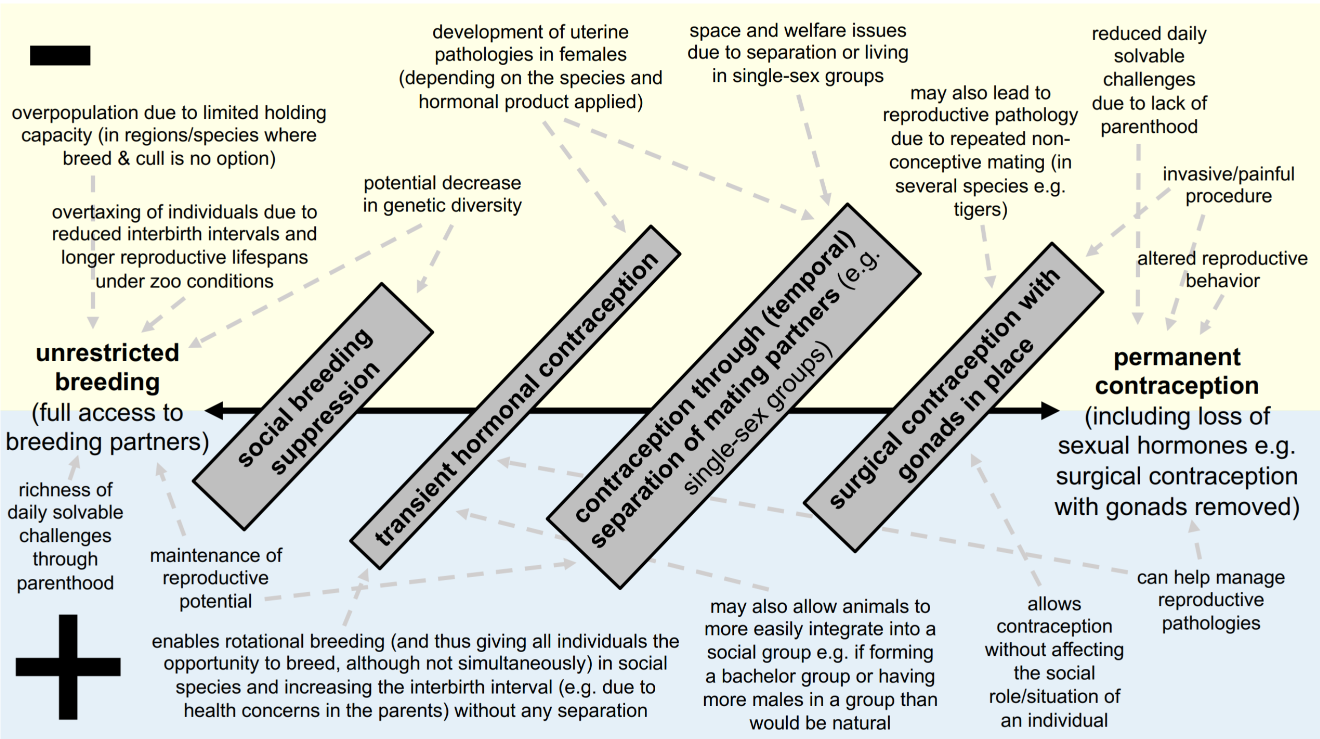

Figure 1. The variety of contraception methods applied in zoo animal husbandry and some potential dis-/advantages

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searching-, mate-choice- and mating-related stress and aggression. Reproductive control methods such as contraception can be used to manage the social dynamics of animals kept in groups. To state some examples of contraception in zoo animal species: castration has been used as a management tool to reduce male aggressive behaviours, allowing group housing or even multimale groups in Japanese macaques (Takeshita et al. 2017), Javan langurs *Trachypithecus auratus* (Dröscher and Waitt 2012), collared lemurs *Eulemur* sp. (Ferrie et al. 2011) and European tortoise species (Hatt et al. 2019). Recently, Taberer et al. (2023) investigated the impact of a gonadotropin-releasing hormone (GnRH) agonist implant as a female contraceptive method on behaviours of adult Guinea baboons *Papio papio*. They found a significant decrease of self-directed displacement behaviours, affiliative and agonistic social interactions, and the duration spent carrying out sentry behaviour, as well as fewer changes of behavioural states, suggesting an enhancement in welfare due to the removal of oestrus, reducing stress for the individuals. These findings are in accordance with a previous study on the relationship between the reproductive cycle and female-female aggression in free-ranging chacma baboons *Papio ursinus* (Huchard and Cowlishaw 2011). Similarly, GnRH agonists were shown to reduce aggressive behaviours in rock hyraxes *Procavia capensis* (Raines and Fried 2016), and GnRH immunocontraceptives prevented African *Loxodonta africana* and Asian elephants from expressing musth periods with heightened aggression (Lueders et al. 2014; 2017; 2019). And given the heightened risk of mortality associated with the rutting period in certain groups, such as cervids (Carisch et al. 2017), zoo managers are likely to consider a suppression of the rut as a way of ensuring survival and welfare in certain species.

Notably, these cases are often, but not always, related to unnatural social group composition, animal density, and spatial confinement, where the potential for evasion is reduced in comparison to natural habitats. For the latter, a recent report promotes the potential of contraception to increase the welfare of wildlife species by putatively reducing animal density, but without considering the direct effect of reproduction suppression on the individual animal (Eckerström Liedholm et al. 2024). Practically, managing intact male dogs, tomcats, stallions, bulls, rams, bucks, boars or roosters is often more difficult, especially in the presence of intact female conspecifics, than managing neutered dogs, gibs, geldings, oxen, wethers, lapins, haviers, barrows or capons. The sheer fact that specific terms exist for the castrated state of male animals underpins how ingrained the manipulation of animal reproduction is in our human culture. Arguably, the life of many of these male animals and their surroundings becomes less stressful once they are castrated, as they are less subject to social and mate competition. Similarly, taking away the necessity of birth or oviposition, and the rearing of offspring, can be considered a reduction of stress for animals when no negative health effects ensue. Rhetorically, one could thus argue that a painless sterilisation is one of the most effective measures of reducing stress in animals provided a significant proportion of their lifespan would be spent engaging in reproductive activity. For surplus animals that originate from breeding populations whose sustainability is granted or not in focus, and that have a clearly defined purpose by human use, whether as production animals for food or as pets for company, the non-reproductive state may represent the most stress-free state of being that leads to the least conflict with common management practices and goals. The fact that in certain husbandry systems, sexual activity and offspring production would be disruptive thus makes reproductive control an important prerequisite for the welfare of individuals living in these systems. Can this be a valid approach to zoo animal husbandry?

Zoo animal purpose

The first question arising from these considerations is that of the purpose of zoo animals. Is their purpose mainly one of display, entertainment and education that justifies measures that manipulate the animals so that husbandry conditions are more easily tolerated without undue stress? Or is their purpose mainly one of species conservation with an inherent need for continuous breeding? The answer to this question may vary between institutions, and between species. On the one side of the spectrum are, for example, species (of populations whose sustainability is granted) used for encounters fostering human health in 'Animal Assisted Interventions' (Sahlin et al. 2019). On the other side of the spectrum are populations managed in breeding programs for long-term sustainability. A major nominal aim of most European zoos today will lie in fulfilling the European Unions' (EU Council 1999) as well as the International Union for the Conservation of Nature's (IUCN SSC 2023) mandate for species conservation, requiring sufficient reproductive turnover. Suppressing reproductive activity in all individuals of a species is therefore usually not a viable long-term option. However, in zoo population management, limited holding space across the institutions that manage a population may lead to the situation that if the population would reproduce at its full capacity (which may even be higher than in free-ranging populations due to reproduction at earlier ages, extended reproductive lifespan and reduced interbirth intervals, and may come with it's own positive or negative impacts on individual welfare), not all animals could be provided with adequate holding space, and hence individuals would have to be killed (i.e., subjected to management euthanasia, 'breed and cull' or 'breed and feed'). This may lead to the limitation of reproduction even in populations whose main aim is long-term sustainability.

In this review, we do not address the question about population management in terms of what proportion of non-reproducing individuals a population can afford while still remaining sustainable, nor do we address the danger of zoo populations managed mainly by reproductive control from becoming over-aged (Clauss et al. 2025). Rather, we restrict ourselves to considerations about the welfare aspect of maintaining individuals while curtailing their reproductive activity, independent of the purpose they are kept for in human care.

Concepts of (zoo) animal welfare

Therefore, we need to address our concepts of animal welfare (Figure 2). Fundamental harm and fundamental anxiety must be rigorously prevented under human care. In the realm of Panksepp's (1998) emotional command systems, this corresponds to the aversive 'fear', 'rage' and 'panic' that we associate with negative affective states, clear distress, and compromised welfare. In our own scheme, this corresponds to the demand that animals in managed care should have an 'anxiety-free' life (Clauss and Schiffmann 2022). This also links to the concept that not all aspects of natural environments (e.g., predation), and not all emotional and physiological capacities of animals, should be replicated or triggered in managed care (Veasey 2018; Browning 2020).

Rather, we need to move 'beyond the Five Freedoms towards A Life Worth Living' (Mellor 2016), aware of an affective experience domain that comprises both negative and positive mental states (Mellor 2017), and engage with those of Panksepp's (1998) emotional command systems that refer to appetitive behaviours of 'seeking', 'lust', 'care' and 'play', and that we associate with positive affective states and eustress. The trigger of such behaviour can be intrinsic, deriving from within the animals (e.g., hunger, or a seasonal motivation to mate), or extrinsic, as a reaction to outside stimuli such as weather, or other animals of the same or other species. Under managed care, these stimuli should ideally never have an intensity that triggers fundamental anxiety but represent eustress, or in other words, 'solvable challenges'. In the realm of feeding, for example, it is no longer considered state-of-the-art to place food so that it can be ingested instantly, in large amounts, at a time; rather, it should be spatially and temporally distributed, and require species-appropriate effort to obtain it (Fens and Clauss 2024). This is because we do not consider the rhetorical 'morphine high', the 'valium numb' or plainly 'nothing to do', i.e. a state of constant, unchallenged, physical wellbeing, as a desirable state of welfare. 'Nothing to do' represents its own kind of distress, giving rise to undesired (stereotypical) behaviours (e.g., Ödberg 1987; Anderson et al. 2010; Lutz 2014) (Figure 2).

When animals solve challenges, they experience that their own actions matter, giving them 'meaning' and 'control', resulting in what we consider a 'meaningful life' (Clauss and Schiffmann 2022). Note that in order to remain true challenges, challenge situations need to comprise some species-appropriate option of failure (without that option being cause of fundamental anxiety). Solving such challenges will foster competence and confidence (Figure 2).

Putting welfare concepts into practice

Applying these concepts in practice leads to the question which of Panksepp's (1998) list of appetitive emotional command systems ('seeking', 'lust', 'care' and 'play') can be used under the logistical constraints of the given husbandry concepts, and which modifications of existing husbandry concepts would be required to allow the use of these systems.

Arguably, assigning value to behaviours is conceptually easy in the domains of nutrition, environment or health, where the motivation of the animal – to feed, rest, to avoid damage – aligns

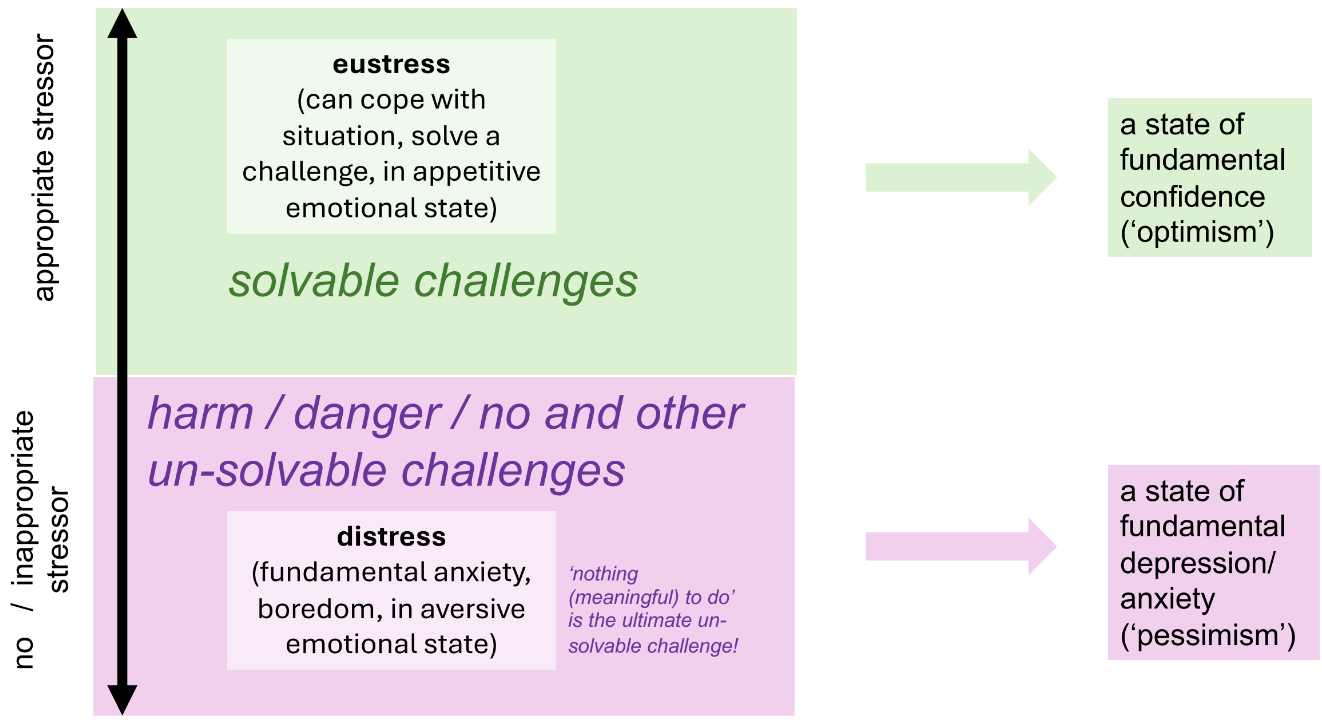

Figure 2. Concept of stressors under managed animal care. A stressor that represents a solvable challenge will cause eustress and may result in an appetitive state. In the long-term, this supports a state of fundamental confidence. In contrast, absent or inappropriate stressors will be perceived as distress resulting in an aversive state. While possibly not detrimental when of rare frequency and mild intensity, when present in the long-term or at higher intensities, these likely support a state of fundamental depression or even anxiety. Note that the absence of any stressor is considered a relevant, un-solvable challenge.

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with our concept of a positive or non-negative experience – finding food, finding a suitable resting spot, being free of damage. In these domains, the initial 'negative affective state', such as hunger, triggers an appetitive 'seeking' motivation (Panksepp 1998) that can be used, when offering food or other environmental components in ways that necessitate species-appropriate problem solving, to achieve a 'life worth living' (Mellor 2016).

Reproduction, by contrast, might be considered somewhat differently. As reviewed by Powell et al. (2024), motivations have not per se evolved to achieve a state of high welfare, but to ensure fitness, defined as reproductive success. Panksepp's (1998) 'lust' and 'care' systems drive animals to seek mating and parental experiences. Yet, these experiences, like mate choice competition, mating, and raising offspring, may also represent stressful and energetically demanding situations. Motivation satisfaction, so to speak, may not automatically align with a state of high welfare in the form of physiological benefit. This creates the dilemma of having to weigh the benefit of the satisfaction of the underlying motivation itself against potential physiological and psychological harm or distress resulting from the reproductive activity – especially if the husbandry concept makes this harm and distress likely (Powell et al. 2024). Thus, certain husbandry concepts that eliminate reproduction and therefore largely preclude the positive use of Panksepp's (1998) 'lust' and 'care' are left only with two emotional command systems – 'seeking' and 'play'.

The attempt to manage animal lives, based on these concepts, in a way that ensures 'net positive balance' of experiences (Mellor 2016; Mellor 2017) faces the challenge of having to fill not only the 24 h of a day, but also the lifetime of an animal with meaningful activity – lives fluctuating between moments of eustress and relaxation, interspersed with rare, accidental incidents of mild distress (Figure 3). What are the practical resources for structuring lives this way? In those private companion dog ownership systems where dog and human share the same space around the clock,

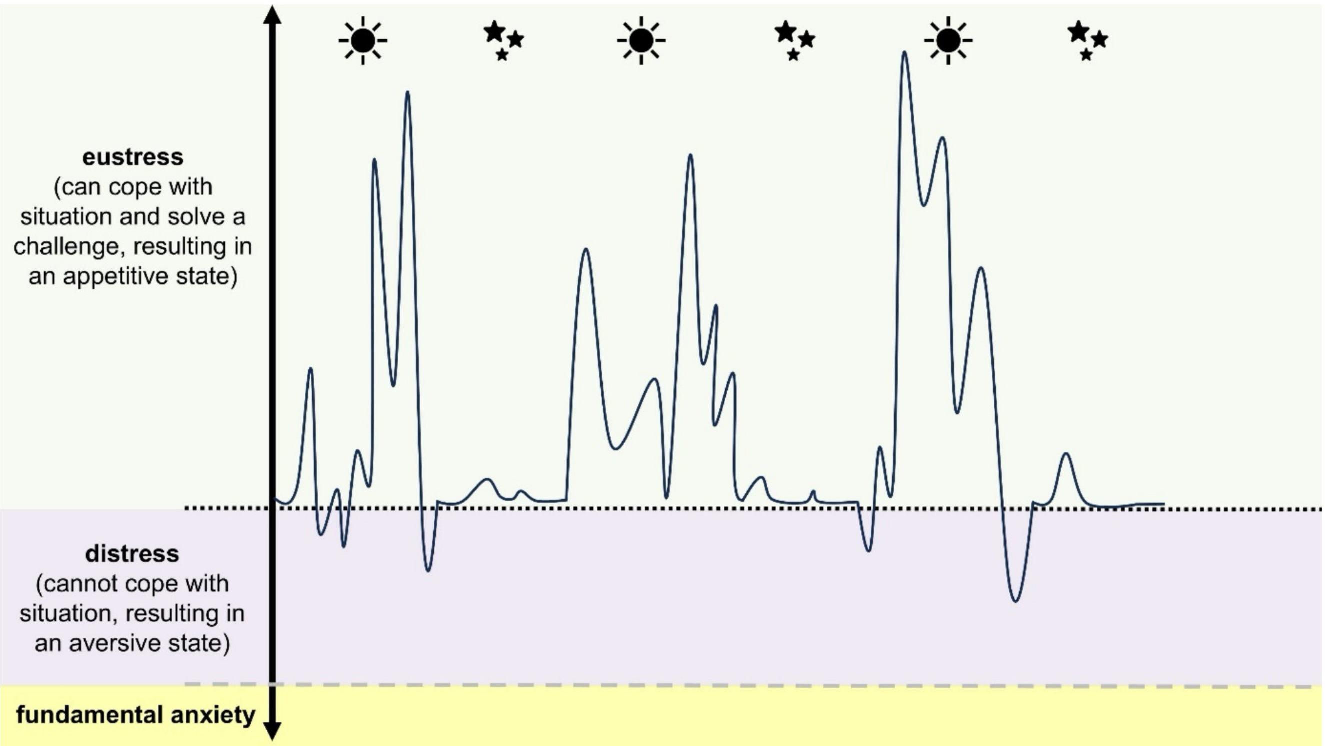

Figure 3. A hypothetical undulating stress level for three consecutive days in a well-managed, diurnal animal as compared to a baseline of relaxation. Note that because of management measures such as appropriate group composition, enclosure design and food provision, stress levels never reach areas of fundamental anxiety. While this graph was inspired by the undulating positive-negative-experience pattern depicted on the Animal Welfare webpage of the Zoo and Aquarium Association of Australasia (https://www.zooaquarium.org.au/public/Public/Animal-Welfare/The-Five-Domains.aspx), the fundamental difference is that challenges (like hunger, separation from mother, environmental disturbance or intraspecific aggression) are not uniformly placed on the negative side of the pattern, but can be positioned within the realm of eustress when they represent challenges the animal can, or has learnt to, solve, and can thus meet without anxiety and aversion but in an appetitive, confident approach. Note that the temporal distribution and intensity of stress peaks is hypothetical and may be different depending on species and husbandry system characteristics.

this seems possible by constant human-animal interaction. In systems of private cat ownership where the cat can roam freely in an environment devoid of apex predators, this is possible through the options for intra-specific contact and inter-specific hunting opportunities, although at the cost of ecosystem disturbance and compromised wildlife welfare (Loss et al. 2022). In zoo animal husbandry systems, where animals cannot roam freely and are without human contact for the majority of the 24 h cycle due to regular working hours, other ways to fill their lives are required.

Here, affiliative interaction with conspecifics, as in sexual and parenting behaviour, represents an important opportunity to fill zoo animals' lives with meaningful behaviour. It is likely that feeding and comfort-related behaviours, and human-animal interaction in the form of training, will not suffice to fill the repeated 24 h cycles that make up a lifetime for many (but not necessarily all) species. Currently, the extent to which social interactions not linked to reproduction with conspecifics – either of the same sex, or as non-reproductive individuals – may be suitable to fill lives with meaningful behaviour is unknown.

Suitability depends on the specific husbandry systems and the context. A husbandry system that aims for species-specific natural interactions and offspring production will aim to offer a stallion

Table 1. Compilation of the aspects to be considered when evaluating the effect of reproduction on zoo animal species by the rough and rather constructional categories "distress" (individual cannot cope with situation, resulting in an aversive state) and "eustress" (individual can cope with situation and solve a challenge, resulting in an appetitive state). Please note that this categorization focuses on the coping capabilities of the individual; therefore a switch from eustress into distress can occur swiftly or even depend on the resources of an individual to cope. Hence, the threshold between distress and a solvable challenge cannot be defined in a general way.

Aspect	Description of behaviour	Distress (–)/eustress (+) of relevance for welfare and explanation	Potential options for substitution where reproduction is prevented
Mate choice and courtship	Female or male choice; seasonal or aseasonal mating; courtship by female and/or male; multiple mating partners or exclusively one defined pair	(+) event of high social relevance (–) competition, e.g. with several males competing for female (–) physically demanding	Ensure a richness of positive and meaningful social interactions. Provide solvable challenges on a daily basis, covering social and physical capabilities of the species. Note that these challenges may include short-term stress for the individual or the social group.
Mating	Only during estrous or also in the absence of reproductive intentions; physically demanding/risky/ painful for mating partners; copulation consensual or rather motivated one-sidedly; mating seems a special event for social group or concerns only mating partners	(+) social event for group (–) physically demanding and potentially harmful (+) short-term positive emotions/feelings (orgasm) (–) short-term negative emotions/feelings (subjugation, pain) (–) can be coercive in some species (painful or even traumatizing)	
Parental / sibling / juvenile care	Nursing, carrying, guarding, protecting, guiding, playing, supporting	(–/+) potentially solvable challenge/ meaningful task during 24/7 for the individuals involved in parenting (–) physically demanding (e.g. reduced rest, decreased foraging)	
Social behaviour and structure	Solitary; monogamous, harem group; mob; family unit; pack; relatedness between group members; temporary or constant social systems	(+) presence of offspring provides solvable challenge to an entire social group (+) presence of offspring stimulates social interaction and cohesion in the group (–) tensions due to changes in the social rank of individuals based on parent status and generation sequence	
Estimated hypothetical part of adult life covered by reproductive activity or impairment of reproductive activity [%]	1-100% depending on species, sex, and social rank. Rough (intuitive) estimate on the percentage of adult life directly covered by reproductive behaviour (courtship, mating, parental/sibling/juvenile care). Aspects indirectly related to, or preconditions for reproductive behaviours (e.g. recovering from the rut in deer species, successful hibernation in tortoises) are not considered here. We tried to take into account that having a longer rearing period may lower the intensity over time as offspring get more independent before the parents breed again.		The higher the proportion the more putatively relevant are compensating measures in case of contraception.

the opportunity to grow up in a herd, spend a certain period of young adulthood gaining social competence in a 'bachelor group' of intact males, and – possibly, but not necessarily – become the breeding stallion of a herd of 'his own'. Castrating this animal in such a system would limit his contributions to the population, but might facilitate his longer participation in a herd or bachelor group, with a range of species-appropriate social interactions, at a longer lifespan (Kirkpatrick and Turner 2007). Yet, this description blends out the question of how offspring production is dealt with in that system, and whether a castrated animal uses up space and resources that could be used for offspring.

In a husbandry system that does not aim for offspring production but is based on the production of surplus animals from some (different, remote) breeding system, such as an animal shelter, not castrating a stallion may actually limit the animal's option more, because it may make socialisation with a herd or a group of geldings more challenging, limiting his opportunity for species-appropriate social interactions and possibly leading to solitary holding.

To sum up these considerations, there are likely constraints of animal physiology, such the impossibility of filling a 24/7 lifetime with only feeding- and comfort-related activity, and constraints of actual husbandry systems, such as an impossibility of 24/7 human-animal interaction. These constraints may make effective behavioural opportunities that truly compensate for a lack of reproductive activity over the lifetime of an animal more challenging, and possibly without an acceptable alternative in specific cases. As an introduction to the comparative aspects of such husbandry questions, we provide a series of examples how animal lives are shaped by reproductive activity.

Reproductive activity: species-specific contributions to lifetime experiences

Apart from a universal motivation to reproduce in all animals, the effect of reproductive activity on the life of animals is inherently species- or even sex-specific. For a somewhat systematic understanding, we first define a set of aspects to consider when assessing the relevance of reproduction (Table 1). These aspects may impact both the individual as well as the entire species-specific social system. In addition, it should be noted that they may not only have immediate but also very long-term welfare impacts. As an example, preventing African elephants from breeding, by temporarily separating the male from the female group during estrous, may mean a short-term negative stress for the male. If such a separation protocol prevents a young female from breeding for a long time, this individual may lose fertility and may not build up her future family herd – a situation which may negatively impact this individual's life for years or even decades by denying her a meaningful activity she could have performed. In order to provide a starting point for comparative discussions, we estimate the percentage of lifetime for either sex of a species that is influenced by reproductive activity.

Thus, we give species-specific examples demonstrating the wide variety of reproductive behaviours in zoo animal species and speculate how these aspects may impact an individual's life, with implicit consequences for that individual's affective states across its lifespan (Mellor 2016) (Table 2). For the proportion of lifetime affected by reproductive activity we estimate ranges from 5% in a female Common cuckoo *Cuculus canorus*, up to 95% in a female Eastern grey kangaroo *Macropus giganteus* (Table 2). For example, the reproductive life of a black-necked swan *Cygnus melancoryphus* consists of lifelong partnership, monogamy, joint brood care and courtship rituals associated to the mating behaviour. Impairing of reproductive function may likely prevent the pair from jointly mastering a relevant solvable challenge, although the pair bond will not inevitably be altered through the prevention of reproduction in these birds (Wilmore 1974; Griffith 2019). A jaguar *Panthera onca*, on the other hand, lives a solitary life with no fixed relationship, showing acceptance of the male by the female only for mating, and the rearing of offspring is done exclusively by females (Baker et al. 2002). Impairing the reproductive function of these animals might affect the life of the female more heavily than that of the male. Red deer *Cervus elaphus* form female groups, living in a harem structure during rut, and the doe alone is responsible for rearing the offspring (Nowak and Paradiso 1991). Impairing reproductive hormone function in this species will affect a major annual event in the life of the males (the rut – which might be positive or negative), and possibly the status of a female in the female group (Clutton-Brock et al. 1986) for a whole reproductive cycle. A bonobo *Pan paniscus* lives in a highly developed group structure, where the sexual act is important for the social structure (Kano 1992). Bonobos are polygamous and perform joint care and rearing of young (Kano 1992). Impairing the reproductive function of certain individuals may or may not upset their position in the social group (Agnew et al. 2016).

Sparse yet naturally occurring infertility (e.g., Packard et al. 1985; Morrow et al. 2002) will affect the welfare of free-ranging animals in ways not yet understood. For certain species, being part of a bachelor herd is part of an individual's life history, may be important for gaining social competence, yet may result in a life of an 'eternal bachelor' with social relationships distinct from those of a breeding individual (e.g., Fischhoff et al. 2009). In other species, social suppression of reproduction by dominant animals may determine the reproductive fate of individuals who often contribute to the raising of the dominant animals' offspring (e.g., Montgomery et al. 2018). Replicating these life histories in managed care may be a relevant contribution to providing animals that do not breed with solvable challenges.

As such, there are large species- and sex-specific differences in the efforts required to compensate for the ensuing lack of meaningful behavioural opportunity when preventing reproduction.

Reproduction related-welfare effects: in sum positive or negative?

Reproductive activity clearly contains elements of distress, such as mate competition, mating activity, labour during birth, energetically demanding lactation or in general the overtaxing of first-time maters and first-time parents (the 'primipara' effect) (Anderson 1986; Snyder et al. 2016; Meyer and Redifer 2024). Obviously, mate choice competition and mating can bear the potential to negatively affect individual welfare due to conflict between competitors, injuries during copulation and reduced feeding and resting during intense courtship. In addition, natural mating may involve sexual coercion (Smuts and Smuts 1993; Clutton-Brock and Parker 1995; McKinney and Evarts 1998; Bisazza et al. 2001; Muller et al. 2011; Feldblum et al. 2014). At the same time, parenthood presents a demanding task with potentially negative welfare effects. As examples, duration of lying rest was distinctly reduced in a primiparous African elephant with a suckling calf (Schiffmann et al. 2020) and in a female giraffe during the peri-parturition phase (Takagi et al. 2019). Undoubtedly, lactation is one of the most energetically demanding periods in a female's life (Gittleman and Thompson 1988; Speakman 2008). Corresponding cortisol peaks, indicators of physiological stress, during the suckling period have been reported in the domestic cat (Alekseeva et al. 2020), and in Asian as well as African elephants during pregnancy, around parturition and during lactation (reviewed in Pokharel and Brown 2023).

Table 2. Exemplary compilation on the wide variety of relevant aspects of reproduction across different species; %time denotes the estimated % of the lifetime activity affected by whether reproductive activity is permitted or not (as described in Table 1).

Species	Sex	Social behaviour and structure	Mate choice and courtship	Mating	Parental care	Further aspects	Conclusions with practical relevance for husbandry	%time	References
Solitary lifestyle with minimum investment in offspring raising by either parent									
Hermann´s tortoise *Testudo hermanni*	Female	Solitary	Mate selection by females	Female choice; have multiple mates	None apart from mating and laying eggs	Seasonal breeding; hibernate during wintertime	Mating and laying of eggs are the only reproduction related behaviours and take place only seasonally. Prevention of reproduction affects only short moments of the life. Physiological health aspects are the main concern (follicular resorption).	5%	1
Hermann´s tortoise *Testudo hermanni*	Male	Solitary	Compete for females by biting	Males compete for females; have multiple mates	None	Seasonal breeding; hibernate during wintertime	Searching for receptive females and mating are the only reproduction related behaviours and take place only seasonally. Competition for reproductive resources may present a solvable challenge or distress depending on the individual and provided access to females.	10%	
Common cuckoo *Cuculus canorus*	Female	Solitary	Make sounds only during mating season	Females have multiple mates	None apart from mating and laying eggs (up to 20) in multiple nests of other bird species. To do so, they visit up to 50 nests.	Seasonal breeding; host parents do the entire parental care	Reproduction related behaviours consist of mating, visiting nests of potential host parents and laying an egg in such nests every other day. These behaviours take place seasonally. Prevention of reproduction affects a seasonally limited time span of a females life.	5%	2
Common cuckoo *Cuculus canorus*	Male	Solitary	Sing and call only during mating season	Males have multiple mates	None	Seasonal breeding; host parents do the entire parental care	Courtship behaviour by calling and singing with subsequent mating are the only reproduction related behaviours and do take place only seasonally. Competition for reproductive resources can also be stressful.	10%	
Solitary lifestyle with minimum investment in offspring raising by one and full investment by the other parent									
Jaguar *Panthera onca*	Female	Solitary	Leave their territory during estrous and call to attract males for mating	Mates with the dominant male present during estrous. Does not tolerate the males´ presence after mating.	Does entire parental care (protection, food, guidance, teaching). Cubs become independent only at the age of nearly two years.	Aseasonal breeding	Caring for offspring and raising them until they become independent presents a nearly life-long task (and thus a solvable challenge) for a female jaguar.	90%	3
Jaguar *Panthera onca*)	Male	Solitary	Males answer the female calls and move to the female.	Males in proximity of a female in estrous compete for mating.	None	Aseasonal breeding	Competition between males for mating presents a solvable challenge (at least for certain individuals).	5%	
Southern cassowary *Casuarius casuarius*)	Female	Solitary	Mate selection by females	Mates with 2-3 different males during one breeding season	None apart from mating and laying eggs	Seasonal breeding	Mating and laying of eggs are the only reproduction related behaviours and take place only seasonally. Preventing reproduction will have little effect on life-long behaviour.	5%	4
Southern cassowary *Casuarius casuarius*	Male	Solitary	Males try to attract females with acoustical cues	Mates with one female	Build nest for the eggs; do the complete incubation and full parental care until the offspring are independent (at about nine months)	Seasonal breeding.	Parental care seems a relevant part of a males life. Preventing reproduction means deprivation of an important part of a males´ life.	75%	

Table 2. Continued.

Species	Sex	Social behaviour and structure	Mate choice and courtship	Mating	Parental care	Further aspects	Conclusions with practical relevance for husbandry	%time	References
Group lifestyle of the parent investing in offspring raising (female), other parent (male) or unsuccessful males are not part of the group									
Red deer *Cervus elaphus*	Female	Live in matrilineal family groups	Synchronized estrous in females of a family group	Mates only with dominant male defending the territory.	Female does entire parental care. For first 7-10 days, calves are hidden and only visited for nursing. Subsequently they follow the mother with the family group.	Seasonal breeding.	Parental care presents a meaningful task during the major time of life in a female deer. Not only the care for offspring, but also the social life in a female group is based on regular reproduction in a deer population.	80%	5
Red deer *Cervus elaphus*	Male	Temporary harem building by territory defence during the rut in fall	Defends the territory against competitors and attracts females to his territory through roaring. During rut, males can lose up to 20% of their body mass and up to 80% of body fat.	Mates with all the females belonging to the harem.	None.	Seasonal breeding.	Reproductive behaviour in the male deer is concentrated in a relatively short time period of the year (rutting season). Considering the physically demanding nature of this period, it is questionable whether such periods can be beneficial for a deer's welfare. Nonetheless, the competition for females provides undoubtedly a (potentially) solvable challenge to the male.	10%	

Table 2. Continued.

Species	Sex	Social behaviour and structure	Mate choice and courtship	Mating	Parental care	Further aspects	Conclusions with practical relevance for husbandry	%time	References
Group lifestyle of the parent investing in offspring raising (female), other parent (male) or unsuccessful males are not part of the group									
African bush elephant *Loxodonta Africana*	Female	Matrilineal family groups remaining consistent for decades	No seeking for males; males visit female groups; females in estrous may attract them through specific calls	Only during estrus (in free-ranging females only every 4-5 years; female choice; highly social event for female groups)	Calves are intensely cared for by mother and allo-mothers/ aunties/sisters of family group;	Parental care for many years and overlapping the birth of the next calf; parental care presents a social task for the family group; life-long mother-daughter bonds	Parental care is a critical part of life for female African elephants. Having a daughter makes a life-long difference for a female African elephant, and preventing reproduction and living together with own female offspring represents a momentous decision for a female elephant.	90%	6
African bush elephant *Loxodonta africana*	Male	All-male groups consisting of individuals out of different age classes; inter-individual bonds may vary in intensity	Guarding behaviour for several days after mating	Highly competitive advertising behaviour with physically demanding musth periods.	No function in parental care, do not live in family groups; no killing of calves by males reported; act as teachers/ guides for sub-adult males	Musth periods with high breeding activity only for a certain amount of time a year (2-3 months) depending on physical condition; matings are possible independent of musth	Due to female choice, successful mating requires social and physical skills; adult males provide guidance to sub-adults during their adolescence and social development. Agonistic social interaction between males may be more relevant than the act of mating as such. Preventing reproduction itself may be less momentous than preventing living together with other (non-related) males.	20%	

Table 2. Continued.

Species	Sex	Social behaviour and structure	Mate choice and courtship	Mating	Parental care	Further aspects	Conclusions with practical relevance for husbandry	%time	References
Group lifestyle of the parent investing in offspring raising (female), presence in group of other parent (male), unsuccessful males solitary // groups									
Eastern grey kangaroo *Macropus giganteus*	Female	Live in mobs with one dominant male, multiple females and several mixed-sex offspring	Unknown	Mated most likely by dominant male	Exclusively by females as long as joey is inside the pouch	Seasonal breeders.	Parental care is very intense due to the constant physical contact between mother and joey. Females can be constantly pregnant having offspring of various age simultaneously. Preventing reproduction in females may have a significant effect on their level of physical stress. Given that most of natural behaviours are shown also with the offspring in the pouch, the effect on activity budgets might be less relevant.	95%	7
Eastern grey kangaroo *Macropus giganteus*	Male	Live in mobs with one dominant male, multiple females and several mixed-sex offspring	Male courts female during estrous	Dominant male most likely individual to mate with females during estrous	Dominant male protects his mob consisting of females and their sub-adult offspring	Seasonal breeders.	Only dominant male gets the opportunity to mate regularly. Per mob there is only one dominant male required. Surplus males may have to leave mob after adolescence, requiring separation in zoos. Preventing reproduction in individual males does not represent a deviation from the natural situation.	10%	
Western lowland gorilla *Gorilla gorilla gorilla*	Female	Stable group consisting of dominant male and several females with their offspring. Offspring leave natal group when reaching maturity.	Unknown	Mate with dominant male in the group.	Does majority of parental care together with group members	Aseasonal breeders.	Parental care for own offspring and those from the group provides a major part of a female's daily activities.	80%	8
Western lowland gorilla *Gorilla gorilla gorilla*	Male	Stable group consisting of dominant male and several females with their offspring. Offspring leave natal group when reaching maturity.	Defends group against competitors	Mates with all females in the group.	Interacts with offspring and is often the preferred adult interaction partner in the group for immature animals	Aseasonal breeders.	Due to his role in the group, the dominant male contributes to the raising of offspring and protects females and youngsters in dangerous situations.	30%	

Table 2. Continued.

Species	Sex	Social behaviour and structure	Mate choice and courtship	Mating	Parental care	Further aspects	Conclusions with practical relevance for husbandry	%time	References
Group lifestyle of the parent investing in offspring raising (female), involvement of other parent in offspring raising (male), unsuccessful males solitary // groups									
Black-necked swan Cygnus melancoryphus	Female	Monogamous pairs with life-long bond	Stay close to each other express sophisticated courtship behaviour.	Only during breeding season. May breed up to three times during reproductive season.	Does the incubation. Cares for hatchlings and carries them on the back. Cygnets may stay with their parents for up to 12 months before becoming independent.	Seasonal breeders. Form larger groups during winter.	Parental care is of increased relevance as a joint effort of the female and the male. Competition behaviours for a mating partner might be less important with respect to the monogamous lifestyle. It seems reasonable to assume that monogamy in various bird species is not exclusively based on reproductive success. The cooperative aspect of monogamy seems to be even more important. Hence, monogamy might present the favorable social system in bird species independent of reproduction. Therefore, we assume that pair bonds may not be altered through contraception.	70%	9
Black-necked swan *Cygnus melancoryphus*	Male	Monogamous pairs with life-long bond	Attacks rivals and defends female. Stay close to each other express sophisticated courtship behaviour.	Only during breeding season. May breed up to three times during reproductive season.	Protects the nest during incubation period. Cares for hatchlings and carries them on the back. Cygnets may stay with their parents for up to 12 months before becoming independent.	Seasonal breeders. Form larger groups during winter.	Parental care is of increased relevance as a joint effort of the female and the male. Competition behaviours for a mating partner might be less important with respect to the monogamous lifestyle.	70%	

Table 2. Continued.

Species	Sex	Social behaviour and structure	Mate choice and courtship	Mating	Parental care	Further aspects	Conclusions with practical relevance for husbandry	%time	References
Group lifestyle of the parent investing in offspring raising (female), involvement of other parent in offspring raising (male), unsuccessful males solitary // groups									
Prairie vole *Microtus ochrogaster*	Female	Some individuals are monogamous, while others seems to breed with several partners	Choose their mating partners based on scent marks.	Continuously breeding, may produce up to one litter every 1.5 months.	Share parental care	Aseasonal breeders.	Parental care seems of increased relevance for both sexes.	80%	10
Prairie vole Microtus ochrogaster	Male	Some individuals are monogamous, while others seems to breed with several partners	Scent marking seems crucial in male-male competition and mate attraction.	Continuously breeding, may produce up to one litter every 1.5 months.	Share parental care	Aseasonal breeders.	Parental care seems of increased relevance for both sexes.	80%	
Parents raising offspring with the support of a larger group of non-reproducing individuals									
Dhole *Cuon alpinus*	Female	Monogamous, cooperative breeder; live in packs with one dominant female and one dominant male	Only dominant female mates with dominant male	Mating several times a day with sophisticated courtship behaviours expressed by specific gestures and vocalizations. Mating seems to present a consensual act.	All pack members support dominant pair in caring for the pups (cooperative breeding)	Offspring show post-independence association with parents	Parental care is of increased relevance as a joint effort of the pack. Competition behaviours for a mating partner are not relevant due to the clear status of the dominant pair. Although not all individuals do reproduce, regular breeding gives social group specific experience and improves the cohesion.	70%	11
Dhole *Cuon alpinus*	Male	Monogamous, cooperative breeder; live in packs with one dominant female and one dominant male	Only dominant female mates with dominant male	Mating several times a day with sophisticated courtship behaviours expressed by specific gestures and vocalizations. Mating seems to present a consensual act.	All pack members support dominant pair in caring for the pups (cooperative breeding)	Offspring show post-independence association with parents	Parental care is of increased relevance as a joint effort of the pack. Competition behaviours for a mating partner are not relevant due to the clear status of the dominant pair. Although not all individuals do reproduce, regular breeding gives social group specific experience and improves the cohesion.	70%	

Table 2. Continued.

Species	Sex	Social behaviour and structure	Mate choice and courtship	Mating	Parental care	Further aspects	Conclusions with practical relevance for husbandry	%time	References
Group lifestyle of the parent investing in offspring raising (female), involvement of other parent in offspring raising (male), unsuccessful males solitary // groups									
Parents raising offspring with the support of a larger group of non-reproducing individuals									
Bonobo *Pan paniscus*	Female	Sophisticated social systems with mixed-sex groups; female offspring leave their natal group during late adolescence	Females seem to prefer partners for mating with which they have a friendly relationship	Females are generally receptive; copulation also during non-fertile periods; females mate with multiple mates except their sons. Mating between group members appears opportunistic and promiscuous.	Female provides most of the parental care	Breeding occurs all the time; paternity seems to include several males with a significant skew to the dominant male in the group Males with her mother in the group have an increased reproductive success. Sexual interactions occur between all age and sex classes of a group and belong to the daily life activities.	Mating occurs independently of fertility. Parental care of relevance for the group in the way of a social task.	90%	12
Bonobo *Pan paniscus*	Male	Sophisticated social systems with mixed-sex groups; male offspring may remain in the group for their entire life	Do not compete for access to females but a linear hierarchy exists, which influences the mating and reproductive success of a male.	Males mate with multiple females of their group, except their mothers. Mating between group members appears opportunistic and promiscuous.	Males may support parental care by providing protection and food to the group	Breeding occurs all the time; paternity seems generally unknown. Dominant males develop amicable relationships with their mates. Sexual interactions occur between all age and sex classes of a group and belong to the daily life activities	Mating occurs independently of fertility. Parental care of relevance for the group in the way of a social task.	30%	

1 (Galeotti et al. 2005), 2 (Nakamura et al. 2005; Jelinek et al. 2014) , 3 (Baker et al. 2002), 4 (del Hoyo et al. 1992) 5 (Mattioli 2011), 6 (Douglas-Hamilton 1972; Wittemyer and Getz 2007; Moss et al. 2011) 7 (Kaufmann 1975; Staker 2014), 8 (Williamson et al. 2013; Tamura et al. 2024) 9 (Paz Silva et al. 2011; Griffith 2019), 10 (Stalling 1990; Getz and Carter 1996; Thomas 2002), 11 (Johnsingh 1982; Fox 1984; Trivedi and Mukherjee 2024), 12 (Williamson et al. 2013; Surbeck et al. 2019; Mouginot et al. 2023)

On the other hand, reproductive activity also holds rewards in the sense of eustress for those individuals that master these challenges, the winners of mate competition, individuals that mate successfully with their intended mating partner (the 'lust' emotional command system; Panksepp 1998), and for individuals that give birth and raise offspring successfully (the 'care' emotional command system; Panksepp 1998); the latter will not only apply for the birthing and nursing parent but, in many species, also for the other parent and a larger social group. As with any challenges, one can claim that individuals make it through periods of variable distress and eustress, provided they have the opportunity and capability to respond to the stressors. They will become more resilient with repetition, which increases the likelihood of eustress in corresponding future situations.

Only very few studies have tried to address the effects of reproductive activity on welfare indicators as compared to the absence of reproductive activity. In individually housed domestic horses, the presence of a foal reduced the prevalence of abnormal behaviours in mares compared to females without a foal on foot (Benhajali et al. 2010). In two different studies on zoo giraffes *Giraffa camelopardalis*, oral stereotypies of a female decreased after giving birth and caring for the offspring (Schüßler et al. 2015; Walldén 2023). A pair of otters *Lontra canadensis* showed distinctively fewer abnormal repetitive behaviours during periods of parenting than periods when they were not caring for young (Island et al. 2023). By contrast, in chimpanzee *Pan troglodytes* groups that contained females with and witout offspring, no differences in abnormal behaviours and in play behaviour between mothers and non-mothers were observed (Cronin et al. 2016); however, apart from play, no other positive behaviours were investigated, there was no comparison within individuals before or after giving birth, and no comparison to groups without any young. Still, mothers had a higher score in 'proximity to young' than non-mothers, indicating that offspring had some social effect. To our knowledge, more systematic studies on the topic are lacking.

There are examples where the presence of sexually intact individuals is important for conflict management in, or the cohesion of, social groups. While sexually driven aggressive behaviours will be eliminated through castration, the absence of one or several reproductive and thus dominant individuals may also increase the overall aggressive behaviours in a social system. This may be particularly relevant in primates, such as golden-headed lion tamarins *Leontopithecus chrysomelas* (De Vleeschouwer et al. 2003), chimpanzees (Ross et al. 2009), Sulawesi crested macaques *Macaca nigra* (Cowl et al. 2021), but has also been shown in African elephants where the presence of dominant males suppressed the abnormal inter-specific aggression of sub-adult individuals (Slotow et al. 2000). It can be suspected that reproductively active or at least physically dominant individuals of both sexes play a crucial role in maintaining social structures based on hierarchies in many other social species. Most importantly, however, parenting and the presence of neonates/juveniles in the group may have a positive effect on the activity budgets of zoo animal species, as shown in Asian elephants (Whilde and Marples 2012; Finch et al. 2021).

Finally, it may be important for juvenile individuals to experience adult conspecifics perform sexual and parental behaviour, and to experience contact to siblings or other young, to develop their own social and reproductive competence (Galef and Laland 2005). In husbandry systems that aim at maintaining population sustainability, this is a crucial consideration.

Whether the sum of these effects, and therefore our intervention into reproduction, is positive or negative is the critical question for a welfare assessment. Ultimately, the judgement about welfare consequences of preventing reproduction will depend on the effects of the applied method on each species under the specific husbandry conditions, e.g. how each member in a functional social group is affected by the (reversible/irreversible) impairment of reproductive function of one or several individuals, or how mating partners are affected by temporal separation during the breeding season. Temporary impairments of reproduction, such as in management systems that apply reversible contraception to prolong the interbirth interval of females, will likely have a lesser effect on welfare than irreversible methods of contraception that eliminate natural reproductive physiology and behaviour. Even within species, there may be different possible outcomes, depending on the individual with its characteristic personality, its social rank and the availability of an appropriate mating partner. Notably, while the 'lust' emotional command system (Panksepp 1998) can be eliminated by some forms of reproductive control, one might argue whether the ensuing absence of offspring is sufficient to eliminate the 'care' emotional command system (Panksepp 1998), possibly leaving an appetitive emotional system unanswered in those individuals of species usually involved in parental care.

Obviously, mate choice competition and mating can bear the potential to negatively affect individual welfare in a significant way due to conflict between competitors, injuries during copulation and reduced feeding and resting during intense courtship (Table 2). In contrast, although definitely demanding for the individual, parental care is rather considered to have a positive effect on welfare – not only because it provides the individual parent or even the entire social unit with a meaningful 24 h task. Caring for offspring might be one of the biggest solvable challenge an animal may face. And if the appropriate species-specific conditions are provided by the husbandry system, a breeding individual will have the capabilities to solve this challenge. Therefore, reducing negative effects related to mate choice competition and mating, but using the positive effects of raising offspring by solitary parents or in social groups, could be considered the combination with the highest welfare benefit. This could also be realised through the use of effective assisted reproductive techniques such as artificial insemination or embryo transfer (Van Den Berghe et al. 2012).

However, evidently, this view hinges on the assumption that parental and social behaviour related to offspring and juveniles is, overall, more positive than an enriched life without offspring or juveniles. The philosophical as well as practical answer to this latter question will determine what we consider to be the best welfare of an individual.

Our human perspective: multiple limitations included

In the discussion about how population management should be performed in the face of limited holding capacity and the requirement of reproductively active and competent individuals, the argument of 'lost opportunity' is often invoked as a reason why even an unexpected death could be construed as a welfare impediment (e.g., Faria 2022). By contrast, the 'lost opportunity' of impaired reproduction is considered less often (but see Penfold et al. 2014; Island et al. 2023) or even actively blended out (e.g., Faria 2025). Possibly, this stems from the fact that preventing reproduction is very common in humans, and that an anthropomorphic idea of fertility control is easily applied to managed animals. This may result in little awareness for the contribution of reproductive activity to a meaningful animal life.

In narratives about curtailing animal reproduction, a common narrative is that the distress of sexual behaviour is avoided (see above). In humans, by contrast, a common narrative is that contraception represents a liberation that allows humans to reap the emotional benefits of sexual behaviour without the burden of offspring production and raising. A comprehensive review of scientific studies in humans – which may not be universally transferrable to other animals – summarizes that maximum life satisfaction and well-being are reached by childless individuals (Hansen 2012). Parenthood may even have a negative effect on life satisfaction at older ages (Bauer et al. 2023). Welfare-reducing effects of parenthood in humans are linked to (i) 'psychological costs, in terms of worries, fatigue, sleep deprivation, and sacrifice and loss of personal freedom', (ii) marital costs in terms of reduced time for the marital couple, (iii) financial costs due to the necessity to provide resources for children, and (iv) opportunity costs where children prevent parents from achieving a career or obtaining further education (Hansen 2012). For zoo animals under human care, reasons (ii-iv) can be considered negligible, and the psychological costs (i) of worries may be reduced by the supportive nature of appropriate husbandry. Evidence in humans suggests fewer negative effects of parenthood in societies that are more supportive in terms of legislation and finances for parents (Hansen 2012). Most notably, humans typically become parents at the expense of other life plans. For zoo animals, arguably, the alternatives to the solvable challenge of reproduction and parenthood may be less bountiful. Even if a creative husbandry provides meaningful alternatives, the practicalities of a zoo animal husbandry may not allow such alternatives to be provided at a sufficient timescale to be effective compensation.

Hansen (2012) explains that humans may confuse happiness – what we would typically equate with 'welfare' in animals – with meaning. The authors state that "meaning can be defined as having a sense of purpose and direction in life, and that one's activities and efforts make sense …", and need not necessarily parallel happiness. We suggest that 'meaning' or 'purpose' can be ensured through the continuous provision of species-specific solvable challenges covering the entire capabilities of an individual animal and considering their biological motivations (Clauss and Schiffmann 2022). Facing such challenges will not only make each day meaningful, but also rewarding with each challenge that can be solved (Van Ree et al. 2000). We believe that this will finally result in a net positive welfare for an individual.

Conclusions

Managed care will always face a conflict between the practicalities of the husbandry system on the one side, and the consequences of reproductive activity – the associated behaviour and in particular the resulting offspring – on the other. There is generally limited conflict with human interests when offering food to animals, as it is a prerogative of keeping them alive. Depending on the husbandry concept, there may be more conflicts of interest when it comes to space, comfort or objects for interaction, as these might require more elaborate and expensive approaches. However, reproduction is the domain where human interests, based on practicality, logistics, and the aversion to kill a certain group of animals, most heavily oppose animal motivation. With respect to reproduction, zoo husbandry concepts may have to include controlled mortality to allow it at a larger scale (Lacy 1991; Walraven et al. 2018; Clauss et al. 2025).

Our review emphasizes the relevance of reproduction as a behavioural complex that can be used to fill the lives of animals in managed care with meaningful activity. To what extent it can be used will depend on whether killing of zoo animals is socially or legally accepted or not (Allen et al. 2023; Allen et al. 2025), because offspring production and holding space limitations are difficult to align perfectly (Alroy 2015; Wilson et al. 2019). For the time being, we encourage assessing welfare of zoo animals not by asking whether they are allowed to reproduce, but whether they are provided with species-appropriate, meaningful, solvable challenges on a continuous basis that corresponds to their biology – or not.

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