

A zoo animal's neighbourhood: how conspecific neighbours impact welfare

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Abstract

While the zoological community strives to provide the best possible living environment for non-human animals, space limitations constrain where zoos can house particular species. Therefore, an individual may live in proximity to animals that impact its behaviour, physiology, reproductive function or overall welfare status. This article examines how solitary and social species living in managed settings are positively and negatively affected by conspecific neighbours. When making housing decisions, zoos should follow husbandry recommendations outlined by zoo associations, integrate natural history information and attempt to view the environment from the perspective of the species of interest. Furthermore, researchers can collect survey, behavioural and physiological data to examine how variables, such as density, distance between neighbours, the age/sex of conspecifics and types/amount of exposure to others influence welfare. Ultimately, zoos should consider the needs of individuals and investigate whether welfare can be enhanced by modifying enclosures, husbandry routines, enrichment schedules or access to conspecifics. A zoo's willingness to alter an animal's exposure to conspecifics may have a substantial impact on physical, mental and emotional health.

Keywords: animal welfare, behaviour, conspecific neighbours, physiology, welfare monitoring, zoo animals

Introduction

In recent years, the international zoological community has boosted efforts to proactively identify and address welfare issues for non-human animals. Organisations, such as the World Association of Zoos and Aquariums (WAZA), the European Association of Zoos and Aquaria (EAZA) and the Association of Zoos and Aquariums (AZA) have called for higher welfare standards within the zoo industry (eg Mellor *et al* 2015). These associations provide member institutions with the resources, guidelines and protocols needed to surpass national and regional welfare legislation. While welfare scientists argue that welfare audits should incorporate animal-based measures that reflect an individual's physical and psychological states (eg hormones, behaviour), the zoo industry has traditionally adopted a resource-based approach that focuses on what facilities provide to the animals (Barber 2009; Butterworth *et al* 2011; Siegford 2013; Whitham & Wielebnowski 2013). For example, to maintain accreditation, zoos are expected to meet certain environmental (eg space, shelter) requirements and follow particular management practices. In addition to these Accreditation Standards, AZA recruits experts to develop taxon-specific Animal Care Manuals (ACMs) that offer husbandry templates and outline best practices for enhancing welfare (AZA 2018; see also Barber 2009). Each ACM considers the natural history of the species and provides recommendations relating to management approaches, diets,

medical treatments, housing arrangements, and the social environment — including any available information about how individuals of particular age-sex classes are influenced by conspecifics. Between the Accreditation Standards and ACMs, zoos place a great deal of emphasis on the living environment for each species. While certain elements of the environment are relatively easy to control (eg water temperature), others are more challenging to manipulate due to factors such as overall available space, exhibit design, existing features and safety considerations.

For instance, because most zoos are constrained by limited space, an individual may live in close proximity to animals that impact its behaviour, physiology, reproductive function or overall welfare status. Individuals sometimes reside in mixed-species exhibits with animals that they would naturally associate with in their wild habitats (Daoudi *et al* 2017). Some “timeshare” their enclosures with members of the same or different species by rotating on/off exhibit during different times of the day (Coe 2004). A considerable amount of research has also focused on the effects of living near predator or prey species. For example, cheetahs (*Acinonyx jubatus*) which live near lions (*Panthera leo*) may experience reduced reproductive success (Hediger 1965). In addition, leopard cats (*Felis bengalensis*) housed in non-enriched enclosures within auditory and olfactory contact of large felids (eg lions, tigers) may exhibit elevated cortisol concentrations, increased stereotypic pacing and

reduced exploratory behaviour (Carlstead *et al* 1993). Far fewer studies have examined how individuals (and groups) are affected by conspecifics living in adjacent enclosures — despite the fact that these housing arrangements are relatively common in a zoo setting. Therefore, while zoos devise unique housing solutions that result in endless combinations of species that live in close proximity to (or even share an enclosure with) members of the same, related or unrelated species, we focus on cases in which animals reside next to conspecifics — a situation that many facilities face but that has not yet been examined in detail.

In this article, we review literature from studies conducted on zoo animals, as well as animals living in other managed settings (eg farms, laboratories, companion animal shelters), on the effects of housing individuals near conspecifics. Since zoos are comprised of diverse taxa that represent different social and mating systems, species are expected to exhibit varying degrees of social tolerance (Kleiman 1994). In fact, as Zajonc (1971; p 144) noted when discussing species-typical spacing patterns:

The average distance between an individual and the nearest conspecific... is as distinct a characteristic of a given species as is its colouring, diet, bone structure, or breeding pattern

Furthermore, species have unique dispersal and territorial patterns (the latter of which may vary by season) that create additional challenges when considering “spatio-temporal deployment” — ie how to house and exhibit animals (Lindburg & Fitch-Snyder 1994). As Lindburg and Fitch-Snyder (1994) point out, these challenges are greatest among species typically characterised as non-social, such as most rhinoceros, bear and felid species. It is also important to note that an individual’s response to neighbouring conspecifics may be influenced by its (and its neighbour’s) age, sex, previous experiences and/or personality. Moreover, even if two individuals of the same species are both negatively impacted by a conspecific, they may display “opposite suites of behaviours” — for example, one may remain silent and inactive while the other may exhibit an increase in vocalisations and pacing (Morgan & Tromborg 2007). Unfortunately, the existing literature is heavily biased toward adult mammals and mainly investigates how animals are negatively affected by conspecifics, such as how neighbours trigger abnormal behaviours and alter reproductive function.

To examine how animals respond to their neighbours, we make a concerted effort to consider a wide range of taxa living in a variety of managed settings, noting any reported sex differences. We also aim to highlight cases in which animals are positively impacted by the presence of conspecifics. Furthermore, we stress that it is crucial for welfare scientists to carefully consider which sensory stimuli are most salient when attempting to understand how an animal perceives its environment. As Morgan and Tromborg (2007; p 265) discuss:

The unfortunate truth is that we are often unaware of sensory elements of the captive environment that animals may find stressful. The sensory stimuli of which we humans are aware are limited, and what is ‘out of sight’ for us may inadvertently stay ‘out of mind’ when considering our animal charges

As noted above, individual differences related to personality or previous experiences are also relevant. Therefore, when discussing approaches for improving the overall living environment for animals housed next to conspecifics, one must consider how recommendations may vary based on species characteristics (solitary vs social, sensory abilities) and individual characteristics (eg sex, age, personality). Figure 1 demonstrates various factors that may affect the impact of neighbouring conspecifics, all of which are discussed below.

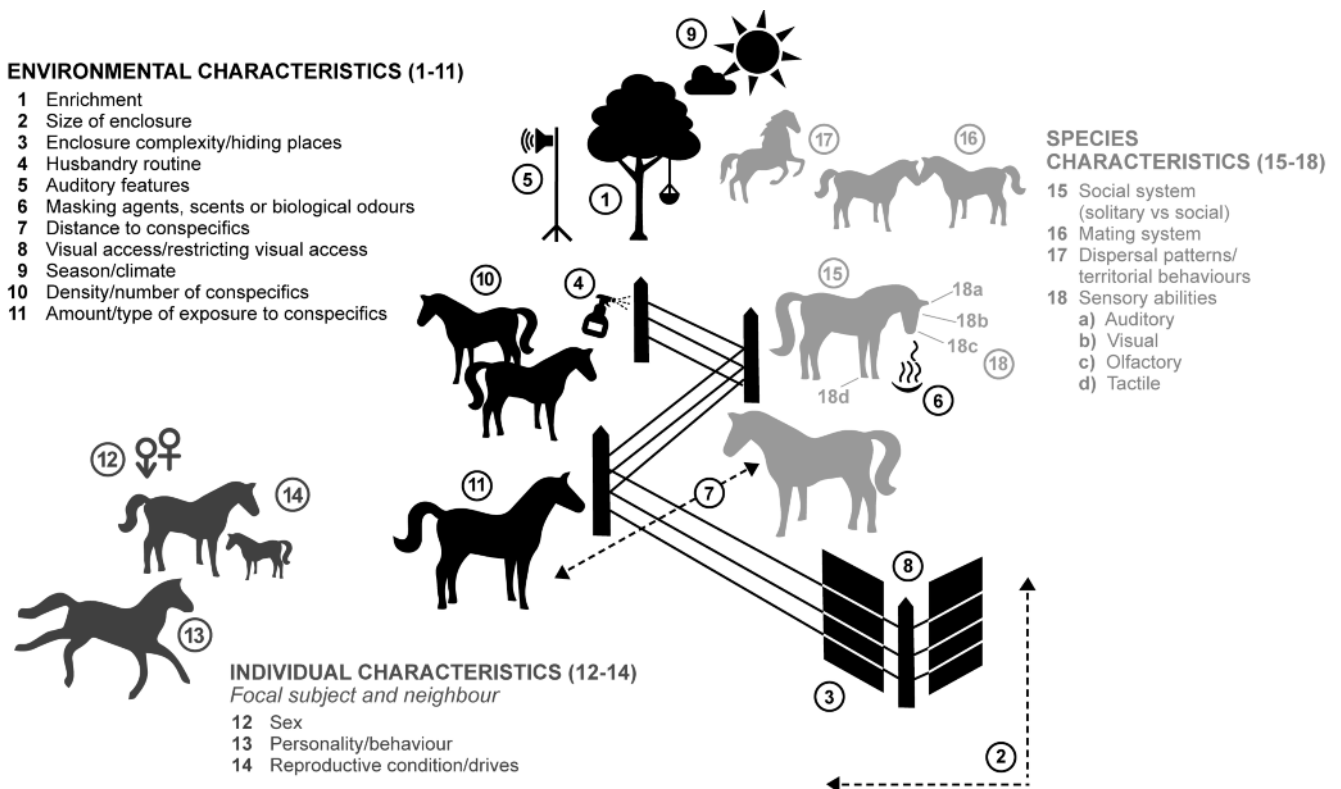
Materials and methods

To review the existing literature that investigates the impact of neighbouring conspecifics, we searched Articles Plus, a research tool that covers hundreds of article databases (eg JSTOR, Science Direct). We began our search with the following terms: (‘neighbor’ OR ‘neighbour’ OR ‘neighbors’ OR ‘neighbours’ OR ‘neighboring’ OR ‘neighbouring’ OR ‘proximity’ OR ‘adjacent’) AND (‘zoo’ OR ‘farm’ OR ‘lab’ OR ‘laboratory’ OR ‘aquarium’ OR ‘agriculture’) AND (‘welfare’ OR ‘wellbeing’ OR ‘well-being’) AND (‘conspecific’ OR ‘conspecifics’). We limited articles to those published in English. This initial search of abstracts resulted in 37 entries. We considered research articles, case studies and literature reviews that examined the environmental, individual and species-related factors that affect the impact of neighbouring conspecifics. We excluded all articles that solely discussed conspecifics living in the same enclosure. We also eliminated studies that involved conspecifics living in adjacent enclosures for only short periods of time (eg during exhibit maintenance). Additional sources were identified by searching the reference sections of these original articles. Ultimately, 58 articles were included in the review.

How conspecific neighbours impact behaviour, physiology and reproductive function

Researchers working in a variety of managed settings have examined how behaviour, physiology and reproduction may be affected by the presence of conspecifics. Most research on both social and solitary species has examined the occurrence of particular behaviours — with the majority of these studies focusing on aggressive, abnormal or repetitive behaviours. In general, there is ample evidence that behaviour can be influenced by olfactory, visual and auditory cues from conspecifics, even if an animal is not directly interacting with others (Morgan & Tromborg 2007). For example, female pigs (*Sus scrofa*) will avoid food dispensers sprayed with the urine of conspecifics which have experienced an aversive or unpleasant experience (Vieuille-Thomas & Signoret 1992; also discussed by Schultz & Tapp 1973 for rats [*Rattus norvegicus*]). Fewer studies have specifically examined the effects of conspecific neighbours on reproductive function. Depending on the species of interest, housing animals near conspecifics may have either inhibitory or stimulatory effects on reproduction due to the exchange of vocal, chemical or visual signals. For instance, mammalian reproductive behaviour and physiology can be influenced by conspecific odours or

Figure 1



Factors that influence the impact of neighbouring conspecifics. Other factors likely play a role but have not been investigated or discussed previously (eg age, rearing history, previous experience). Please see the following articles to learn more about each potential factor (additional studies are referenced in the text): 1) DeBoer *et al* 2015; 2) Carlstead *et al* 1999a; 3) Miller *et al* 2008; 4) Carlstead *et al* 1999a; 5) Kleiman 1994; Carlstead *et al* 1999a; 6) Kleiman 1994; 7) Zajonc 1971; 8) Miller *et al* 2008; DeBoer *et al* 2015; 9) Carlstead *et al* 1999a; Bennett *et al* 2015; 10) Carlstead *et al* 1999a; Garner *et al* 2006; Bennett *et al* 2015; 11) Herskin & Jensen 2000; Brown *et al* 2016; 12) Orgeldinger 1997; Carlstead *et al* 1999a; Bennett *et al* 2015; 13) Palya & Zacny 1980; Cooper & Nicol 1994; Videan *et al* 2005; 14) Carlstead *et al* 1999a; Bennett *et al* 2015; 15) Zajonc 1971; Kleiman 1994; Lindburg & Fitch-Snyder 1994; 16) Kleiman 1994; Lindburg & Fitch-Snyder 1994; Carlstead *et al* 1999a; 17) Kleiman 1994; Lindburg & Fitch-Snyder 1994; Orgeldinger 1997; 18) Kleiman 1994; Orgeldinger 1997; Carlstead *et al* 1999a; Kuhar *et al* 2003; Brown *et al* 2016.

pheromonal cues (Wasser & Barash 1983; Kleiman 1994). Effects include the timing of puberty, inhibiting/promoting sexual activity and preventing implantation. For some species, forced and constant proximity to others may result in ongoing adrenal activation, ultimately leading to reproductive suppression. This response can manifest in various ways, including delayed sexual receptivity, delayed ovulation or failure to display signs of behavioural oestrus (eg Wasser & Barash 1983; Lindburg & Fitch-Snyder 1994; Wielebnowski *et al* 2002). In extreme cases, the physiological effects of social stress may lead to sustained “psychological castration” (term coined by Brown 1978). However, even individuals of many solitary species need the opportunity to familiarise themselves with conspecifics of the opposite sex to promote reproduction. It is therefore necessary to determine the optimal amount and types (visual, olfactory, etc) of exposure, especially because being in close proximity to a potential mate can lower the drive to reproduce for species in which novelty is sexually stimulating (Lindburg & Fitch-Snyder 1994). We will review literature regarding how conspecific neighbours

influence behaviour, physiology and reproductive function — first for social species, then for animals traditionally described and managed as solitary. Whenever possible, we will include literature from other managed settings, including farms, laboratories and companion animal shelters, although we acknowledge that animals in these settings sometimes live in environments that are less stimulating and enriched than modern zoo enclosures. An animal that has access to an enriched, stimulating environment may be less sensitive or reactive to its neighbour.

The impact of conspecific neighbours on social species

Individually housed social animals

There is some evidence that housing social animals alone, but in visual or limited physical contact with conspecifics, may be associated with indicators of poor welfare. In a paper examining the behavioural problems of zoo equids, Boyd (1986) reported that a Przewalski’s horse (*Equus ferus przewalskii*) stallion paced to the point of exhaustion whenever he had visual access to foals in an

adjacent enclosure. In a study of castrated male piglets, those that only had visual access to others exhibited more negative behaviours (eg increased frequency of pawing, decreased frequency of play behaviour) than those which could interact through mesh barriers or were group-housed (Herskin & Jensen 2000). Similarly, although DeBoer and colleagues (2015) found that pigs housed in visual isolation exhibited greater tear-staining and lower eosinophil levels (both considered measures of poor welfare) than those with visual access to conspecifics, the researchers found no differences when comparing the time budgets of these treatment groups. In fact, when examining postural behaviour, those housed in visual contact with other pigs actually spent more time lying sternally — a posture that reflects reduced restfulness — than visually isolated pigs. Furthermore, those with visual access to others had higher cortisol levels if they were housed without enrichment (eg rubber mats, mirrors) than if they had access to these objects. The authors suggest that:

The increase in cortisol... may be due to frustration caused by an inability of the pig to bring itself in closer proximity to the companion seen across the way

but that enrichment has positive, moderating effects (p 24). For social animals, limited access to conspecifics may even impact reproductive function. Indeed, a multi-institutional epidemiological study of the North American zoo elephant population (*Elephas maximus* and *Loxodonta africana*) found that social isolation, with or without restricted physical access (ie the ability to interact through a barrier), increased the likelihood of ovarian acyclicity in African elephants (Brown *et al* 2016). In sum, housing social animals individually, with limited visual or tactile access to conspecifics, may have negative effects.

By contrast, some studies have shown that providing individually housed social animals with visual access to conspecifics may be beneficial, reducing the incidence of abnormal and stereotypic behaviours. For instance, questionnaire data revealed that yearling and adult racehorses (*Equus ferus caballus*) given visual access to other stables were less likely to perform abnormal behaviours, especially wood-chewing, than those unable to view other horses (McGreevy *et al* 1995). These results are supported by an experimental study conducted by Cooper and colleagues (2000) who examined how short-term (five-day) changes in stable design impacted the performance of stereotypic weaving for geldings (n = 10). These researchers found that offering additional fields of view reduced stereotypy and that the strongest effects were found when side portals (with grills) were opened, allowing the horses to see into neighbouring stalls. In fact, simply providing mirrors may reduce the effects of social frustration and/or isolation. McAfee and colleagues (2002) discovered that horses (n = 4 geldings; 2 mares) known to engage in stereotypic weaving were less likely to exhibit weaving, head-nodding or head threats when provided with a mirror than when living in unmodified stables (see also Mills & Davenport 2002). This reduction in weaving persisted throughout the five weeks of the study.

Having visual access to neighbours may also be beneficial to social birds housed in a laboratory setting, as stereotypy was negatively correlated with number of neighbours for orange-winged Amazon parrots (*Amazona amazonica*; n = 32 males; 32 females) (Garner *et al* 2006). Similarly, dog (*Canis familiaris*) welfare researchers have argued that providing domestic dogs with visual intraspecific contact can offset the negative effects of single housing in shelters (Wells 2004). For certain social species living in laboratories, farms and shelters, there is support for providing individually housed animals with visual access to conspecifics.

When examining whether visual access to conspecifics is beneficial or detrimental, it is crucial to consider the neighbour's behaviour and personality. Numerous studies have investigated how the stereotypic behaviour of conspecifics negatively impacts the behaviour of individually housed animals living in laboratory or farm settings. Cooper and Nicol (1994) found that newly weaned, non-stereotyping bank voles (*Clethrionomys glareolus*) housed in transparent cages next to a stereotypic demonstrator were more likely to develop stereotypies than those housed in opaque cages next to a stereotypic demonstrator or next to a non-stereotypic demonstrator. Unfortunately, these stereotypies persisted even after being transferred to opaque cages. Similarly, non-stereotyping (ie naïve), food-restricted pigeons (*Columba livia*) developed stereotypic behaviours within five days of being surrounded by two stereotyping neighbours (Palya & Zacny 1980). Naïve, food-restricted pigeons housed between non-stereotyping neighbours did not develop stereotypic behaviours. For pigs, Appleby and colleagues (1989) found that gilts performed similar amounts of stereotypic behaviour as neighbouring sows (see also Appleby & Lawrence 1987). While imitation cannot be ruled out, the authors argued that the gilts were likely stressed by the stereotypic behaviour exhibited by their neighbours. Indeed, the strongest correlations were found between the gilts' total repetitive behaviour and the most noisy, conspicuous behaviour of the neighbours (repetitive chewing/manipulating of the tether chains) rather than between particular types/categories of stereotypies. Similar results have been found for horses. Survey data revealed that housing horses next to aggressive or stereotypic neighbours increased the likelihood of crib-biting, wind-sucking and weaving (Nagy *et al* 2008). As a result, the authors recommended that individuals susceptible to developing stereotypies not be housed near "stress agents," such as stereotypic neighbours. Experiments carried out by Ninomiya and colleagues (2007) support these survey data: horses housed in stalls that faced one another displayed more weaving than those housed in a straight line. The authors suggest that social learning may be at play. Whether the development of stereotypic behaviours is stress-induced or involves mechanisms of social transmission (eg social learning, stimulus enhancement), stereotypic neighbours can negatively impact the behaviour of conspecifics.

Group-housed social animals

Several zoo studies have examined the effects of housing groups of primates in close proximity to unrelated conspecifics. In a study of family groups of siamangs (*Hylobates syndactylus*), those housed near conspecifics spent more time duetting than those without neighbours (Orgeldinger 1997). Orgeldinger noted that the songs function as a form of territorial defence and suggested that the duetting represents a “ritualised acoustical fight” or a “show of strength”. The author also pointed out that while adult males are, in general, more attentive to and impacted by external factors (including conspecifics) than adult females, female territorial behaviour was specifically triggered by the sound or sight of other females. Most of the other research on zoo primates has focused on callitrichids, which are known to experience abortions and infant loss when living in colonies (see Olsson & Westlund 2007). Kleiman (1994) reported that golden lion tamarins (*Leontopithecus rosalia*) living in a zoo breeding facility became agitated by other family groups and emitted alarm calls and other vocalisations indicative of high arousal. Even though groups were separated by one-way glass doors and did not have visual access to one another, the air handling units transmitted odours and sounds. These doors also acted as mirrors and evoked aggressive displays and alarm calls. In a study of Geoffroy’s tamarins (*Saguinus geoffroyi*), Kuhar and colleagues (2003) found that tamarins housed in a colony with auditory, olfactory and limited visual access to other groups displayed higher levels of aggression and lower activity levels than those living in non-colony groups (ie those with no visual, olfactory or auditory contact with other groups). Furthermore, there was a trend for individuals in colonies to perform more scent-marking, huddling and sexual behaviours. The authors noted that a large proportion of aggressive acts were directed at neighbours and mating behaviours usually followed these inter-group interactions. Furthermore, they argued that the failure to drive away competitors and resolve these territorial conflicts likely leads to social stress and contributes to the infant abuse that occurs in colony situations (Kuhar *et al* 2003). Clearly, for some primate species, attempts should be made to prevent visual interactions, to reduce auditory communication (eg use radios/white noise) and to mask conspecific scents (eg introduce “biological odours” such as plants) (Kleiman 1994).

There is also evidence of neighbouring groups positively influencing the behaviour of conspecifics. In a study of “neighbour effects” and social contagion in laboratory-housed chimpanzees (*Pan troglodytes*), Videan and colleagues (2005) found that the vocalisations emitted by neighbouring groups not only impacted the rates of aggressive behaviours performed by focal groups but also the rates of affiliative behaviours. Similar to previous studies of chimpanzees (eg Baker & Aureli 1996; Schwandt *et al* 2000), the authors discovered significant relationships between the frequency of agonistic noises/vocalisations and the rates of various aggressive behaviours (bluff displays, pant-hoot vocalisations and contact aggression). However, they also found that grooming vocalisations from neighbouring groups were positively associated with grooming

behaviour and vocalisations of focal animals. It is worth noting that groups were only in auditory contact, without visual access to one another. The authors stress that managers should closely monitor the compatibility of neighbouring groups, as behaviours both positive and negative can be triggered throughout the colony.

There is still much to be learned about how social animals — whether housed alone or in groups — are affected by neighbouring conspecifics. The research described above examined both exotic and domesticated animals and covered a wide array of settings and species (eg equids, ungulates, primates, birds). Even when studies examined the same species, there were great methodological differences, including which age-sex classes were included. As discussed in more detail below, large-scale studies should be conducted for particular species to determine how variables, such as distance from, types of access to, and the age/sex/behaviour of neighbouring conspecifics influence welfare. Researchers and caretakers also should attempt to improve the welfare of individual animals by modifying the enclosure or routine — whether that means providing more or less access to conspecifics — and then collecting additional data to assess the impact of these changes.

The impact of conspecific neighbours on solitary species

A handful of zoo studies have specifically investigated the effects of housing solitary species in close proximity to conspecifics. Bennett and colleagues’ (2015) study of okapis (*Okapia johnstoni*) revealed that in the summer, an animal’s number of neighbours was positively correlated with its rate of pacing. The authors suggested that while female pacing mainly seemed to be anticipatory in nature, male pacing may also reflect an unfulfilled drive to gain access to reproductive females. A case study of an adult female okapi determined that constructing a visual barrier to block her view of males in neighbouring stalls led to a significant decrease in head-rolling behaviour (Troxell-Smith & Miller 2016). Furthermore, the zookeepers reported — via survey responses — a decrease in negative behaviours (eg pacing, anxiety, head-rolling), an increase in positive behaviours (eg interest in the environment), and an improvement in overall welfare. The authors pointed out that this elusive species lives in dense forests and that individuals likely do not encounter conspecifics on a regular basis. They suggested that even minor modifications to enclosures, such as erecting a few slabs of plywood, may help zoos, “more thoroughly represent the social situation experienced by okapi in their native habitat” (p 40). Clearly, it is crucial to consider a species’ natural history when making management and housing decisions.

Several zoo researchers have examined the impact of housing tigers (*Panthera tigris*), traditionally managed as solitary animals but not well-studied *in situ*, near conspecifics. For instance, De Rouck and colleagues (2005) distributed questionnaires to 93 European zoos that cared for tigers and determined that the occurrence of pacing was higher for individuals and pairs housed next to conspecifics

than for those not bordering conspecifics. In addition, the researchers conducted behavioural observations on a subset of females ($n = 15$) and found that those which paced frequently had neighbours which paced frequently as well. It is possible that the pacing was triggered by the behaviour of stereotypic neighbours, as discussed above for bank voles (Cooper & Nicol 1994) and pigs (eg Appleby *et al* 1989), or by being exposed to the same environmental stimuli. The authors suggested that pacing may also be sexually motivated and reflect frustration caused by the animal's inability to interact with neighbours (see also Clubb & Mason 2001). This study also investigated the occurrence of head-to-head rubbing — a behaviour assumed to reflect a relaxed state — and found that while pairs without neighbours engaged in this behaviour relatively frequently, pairs with neighbours never rubbed heads. De Rouck and colleagues argued that although tigers may not be as solitary as once thought and may benefit by being housed in pairs, neighbouring conspecifics are likely a source of stress. They, therefore, recommended that zoo managers appropriately space members of this species and, if necessary, erect visual barriers.

Recent studies on tigers have specifically investigated the effectiveness of visual barriers designed to obstruct views of conspecifics. Bashaw and colleagues (2007) conducted a case study on one female tiger by placing a visual barrier between the study subject and her holding area to reduce exposure to “social stimuli” (from both conspecifics and zookeepers). However, the visual barrier actually led to an increase in the frequency of pacing. As a result, the authors argued that large felids may be negatively affected by their inability to control their exposure to various forms of social stimulation and suggested that exhibits include barriers that limit visual, auditory and olfactory access. Of course, it is important to remember that the barrier was placed between the tiger's enclosure and the holding area; where there was likely a high level of zookeeper activity (eg diet preparation). In an experimental study conducted by Miller and colleagues (2008) that assessed the effects of visual barriers in six female tigers, individuals paced more when they could view neighbouring conspecifics. Specifically, the researchers erected a visual barrier during the first half of the day and removed it in the afternoon and found that pacing duration only differed from baseline (ie was lower) during the former condition. Similar to what De Rouck and colleagues (2005) argued for tigers, and DeBoer and colleagues (2015) argued for pigs, the authors suggested that pacing likely reflects frustration stemming from the animal's inability to directly interact (either positively or negatively) with neighbours (see also Mason *et al* 2001, 2007).

For some species, barriers that impede tactile, auditory or olfactory communication may negatively impact reproductive function. For instance, Carlstead and colleagues (1999a,b) investigated the effects of housing black rhinos (*Diceros bicornis*) in sub-optimal social situations, as well as the interference caused by various types of barriers. Black rhinos, typically described as a solitary species with overlapping home ranges, face many challenges in zoos

including delayed first reproduction, lengthy inter-birth intervals and even failure to reproduce (Carlstead *et al* 1999a). Carlstead and colleagues (1999a) discovered that the density of females at a facility influenced reproductive rates, with those housed in proximity to other females giving birth to their first offspring approximately three years later than sole females. Furthermore, females living in heavily walled enclosures demonstrated relatively high levels of chasing, stereotypy and mouthing — behaviours not only indicative of agitation but also negatively correlated with breeding success (Carlstead *et al* 1999b). The authors argued that these barriers prevent individuals from observing and physically interacting with, or escaping from, conspecifics that are still in olfactory and auditory contact (though some types of walled enclosures even interfere with auditory communication). Interestingly, for male black rhinos, these same indicators of behavioural agitation (chasing, stereotypy and mouthing) were associated with the frequency of chlorine use, suggesting that males may become disturbed when olfactory communication with neighbouring females is disrupted (Carlstead *et al* 1999a). Indeed, chlorine may prevent males from detecting females in oestrus by masking, altering or removing odours or even by damaging males' mucous membranes. This study demonstrates the importance of considering all of the senses that may be relevant to the species of interest as well as any potential sex differences.

As with social animals, relatively little is known about how solitary animals in a zoo setting are influenced by conspecifics housed in adjacent enclosures. While curators and zookeepers share anecdotes about how neighbouring conspecifics impact behaviour and physiology, surprisingly few studies have specifically examined this topic. For species that do not breed successfully in zoos, researchers should consider whether neighbours might have inhibitory effects on reproductive function. It is possible that the vocal, chemical, visual or even tactile signals emitted by neighbours — especially those of certain age-sex classes — influence the timing of puberty, cause delayed ovulation, prevent implantation, increase the likelihood of abortions or suppress reproduction in other ways. Researchers should conduct multi-institutional studies for particular species to examine how neighbouring conspecifics affect behaviour and reproduction, as well as how manipulating certain variables (eg visual access, husbandry practices) may enhance reproductive output and overall welfare.

Animal welfare implications and conclusion

To better understand the positive and negative effects of housing zoo animals near conspecifics, researchers should conduct multi-institutional studies for particular species. However, before initiating a study — and in order to determine which behaviours to examine or which elements of the environment to manipulate — it is necessary to consider the species' natural history. How often are individuals of a particular sex in visual, auditory, chemical or tactile contact with conspecific males and females? Does

the answer to this question vary depending on the season? If breeding is desired, is novelty essential to its success? When designing a study, it is also crucial to think about which senses are relevant to the species of interest. Unfortunately, relatively little is known about the auditory profiles of most species, some of which have the ability to detect ultrasonic or infrasonic sounds (Morgan & Tromborg 2007). It is also important to remember that nearly all mammalian species are macrosmatic, meaning that they rely heavily on olfactory cues (Slotnick *et al* 2005). In fact, chemical communication is vital to the expression of normal social and reproductive behaviour for many species (Morgan & Tromborg 2007). As demonstrated by Carlstead and colleagues (1999a), variables such as “frequency of chlorine use” may be key when examining abnormal behaviours or even breeding success. The proximity between conspecifics — and various forms of signal degradation that may occur due to distance, environmental noise or physical barriers — is also relevant. In sum, the researcher should attempt to view the environment and daily routine from the perspective of the species of interest.

For many species, it may be beneficial to collect survey data before initiating behavioural, physiological or experimental studies. By starting with survey data, one can examine how variables, such as density of males/females, distance to neighbouring conspecifics, the age/sex of these neighbours, various types of access (eg visual, tactile), husbandry practices (eg use of white noise), and size/attributes of the enclosure (eg walls) may impact welfare. In terms of behaviour, staff can report whether individuals perform certain stereotypies or abnormal behaviours and also provide an estimate of the amount of time spent engaged in these behaviours. Surveys can be followed up with behavioural research designed to generate activity budgets for behavioural states and to calculate rates for particular behavioural events. If possible, researchers should identify the context in which behaviours are performed and attempt to assess the behaviour of neighbouring individuals. After all, the intervention for an animal which paces due to social learning (eg a visual barrier) may differ from the approach one would take for an animal expressing frustration due to its inability to monitor a neighbour (eg providing a ‘window’ into the adjacent enclosure). Of course, it is also crucial to include behavioural indicators of good/great welfare, such as inquisitive exploration, positive vocalisations and behavioural diversity (Miller *et al* 2016). For social animals that are not housed individually, researchers can incorporate affiliative behaviours (eg allo-grooming) and social play (for a review, see Boissy *et al* 2007; Whitham & Wielebnowski 2013). Finally, behavioural measures should be complemented with physiological measures whenever possible. For instance, researchers can include non-invasive assessments of hypothalamic-pituitary-adrenal axis (HPA) activity (eg faecal hormone monitoring) and autonomic nervous system (ANS) activity (eg measures of heart rate, body surface humidity, peripheral body temperature) (Whitham & Wielebnowski 2013; Whitham & Miller 2016). The ultimate goal should be to

regularly monitor as many measures of physical, mental and emotional health as possible for individual animals.

The next step is to investigate whether behavioural and physiological measures of welfare can be manipulated (improved) by altering enclosures, husbandry routines, enrichment schedules or types/amount of access to conspecifics. For some highly social species, an intervention may be as straightforward as reducing the amount of time spent alone or in limited visual/tactile access to conspecifics. For example, because African elephants live in sophisticated fission-fusion societies, it is crucial that individuals regularly have opportunities to engage in affiliative behaviours and co-ordinate their movements/activities with herd-mates throughout the day (Brown *et al* 2016). Separations should be short-term and infrequent if possible. For animals that appear to be negatively impacted by conspecific neighbours and cannot be relocated due to space limitations, animal care staff may decide to implement particular types of barriers, masking agents or sound-proofing methods. These modifications should be based on the species’ natural history, seasonal requirements and characteristics of the individual and neighbour (eg age, sex, personality, previous experiences). An alternative approach to overcoming space constraints may be to increase complexity within the enclosure (Miller *et al* 2008). Indeed, Mellen and colleagues (1998) found that for small felids, exhibit complexity, which provided hiding places from other cats in the same enclosure, was negatively associated with pacing. We encourage zoos to brainstorm solutions for overcoming space limitations and minimising an individual’s exposure to neighbours, such as enhancing an animal’s ‘vertical experience’ by providing platforms and offering additional access to holding areas.

It is also possible that an animal will habituate to its neighbour over time and that this process can be accelerated by employing techniques used for animal introductions, such as exposing an individual to the scent of the conspecific or slowly encouraging positive interactions via a “howdy door” (Powell 2010). However, it is important to remember that the needs and preferences of an animal and its neighbour may be unique and even contradictory, especially when males and females with differing reproductive strategies are housed near one another. For instance, black rhinos exhibit sex differences in sensitivity to environmental factors, with males being more affected by overall space allowance and the olfactory environment, and females by visual and/or acoustic interference caused by certain types of walled enclosures (Carlstead *et al* 1999b). On a similar note, while an individual might benefit from being given the opportunity to control aspects of the environment (eg types/amount of access to conspecifics), the neighbour also must have the ability to make choices about how and when to interact.

Ultimately, the zoo community’s goal should be to fine-tune species-specific recommendations for housing individuals of particular age-sex classes. Each Animal Care Manual (ACM) includes a sub-section that discusses the ‘Influence of others and conspecifics’ as well as a disclaimer that the manual, “should be considered a work in progress, since

practices continue to evolve through advances in scientific knowledge” (eg AZA Gruiformes TAG 2009; p 2). Whenever possible, guidelines regarding the housing and spacing of conspecifics should be based on data from multi-institutional, systematic studies.

In sum, a zoo’s quest to improve the welfare of individual animals must include an assessment of the effects of forced proximity to conspecifics. Exposure to conspecific neighbours may be one of the most salient features of the living environment for many species, whether solitary or social. While animal care staff can create and follow general rules of thumb for a species based on AZA’s recommendations, natural history information and survey data, management should do its best to consider the needs and preferences of individual animals when making housing decisions. While facilities often have limitations in terms of location or space, individual animal welfare can be enhanced by modifying elements of the environment or the husbandry routine. The success of these interventions can be evaluated by collecting behavioural and physiological data; bearing in mind that additional assessments may be required as seasons change, an animal ages, reproductive condition changes or a new neighbour is introduced. For facilities that plan on renovating or creating new exhibits, master site planning should involve detailed, evidence-based discussions about how best to house particular species when conspecifics will be in close proximity to one another. A zoo’s commitment to understanding how an individual perceives its living environment, and the willingness to make even minor adjustments to that animal’s exposure to conspecifics, may have lasting and widespread effects on physical, mental and emotional health.

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