

Research article

# Swipe right to match the stripes - pair compatibility in the okapi ex-situ programme: A look at male aggressive behaviour during breeding introductions

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## Abstract

Zoo population management programmes can safeguard genetic diversity and ensure the survival of endangered species. The selection of mates for achieving genetic and demographic goals within the managed population means that free mate choice is very limited. This lack of choice may lead to pair incompatibility among the selected pairs, which have the potential to undermine the whole programme due to low reproductive outcomes. In the okapi *Okapia johnstoni* ex-situ programme in European zoos, cases of male aggression during breeding introductions have been attributed to a lack of compatibility among the pair. However, very little is understood about which factors are linked to the occurrence of this behaviour. In this study, a questionnaire was sent to zoos holding okapi, requesting information about the mating behaviour of their pairs and husbandry aspects. Subsequently, the occurrence of male aggression in the pairs was analysed against age difference, female oestrus management and socialisation of both individuals at a young age. Age difference and socialisation did not explain the occurrence of male aggression. Instead, the female oestrus management chosen for each pair was a significant factor predicting the occurrence of male aggression. Pairs that were allowed together regularly during the female's anoestrus period displayed significantly fewer aggressive behaviour compared to those that were only given access during the female's oestrus. We suggest that regular introductions might promote familiarity and the exchange of important reproductive cues among the pair, which leads to successful breeding introductions. However, based on our results, we cannot determine whether the two different oestrus husbandry approaches cause the occurrence of aggression or whether the occurrence of aggression influences which husbandry is applied to any given pair. We believe that the keeper's perception of pair compatibility may be a confounding factor in our results since keepers are often hesitant to introduce animals outside of the female's oestrus if they perceive the pair as incompatible or if aggression has occurred. Similar animal keeper biases have been documented in other breeding programmes, and further research is needed to better understand pair compatibility in okapi.

## Introduction

The contribution of population management programmes in zoos has been widely recognised as crucial against biodiversity loss (IUCN 2023). This contribution is based on education, keeping genetic and demographic backup populations, and direct support for in-situ conservation (Conde et al. 2011; Conway 2011; Lees and Wilcken 2009; McGowan et al. 2017; Zimmermann 2010). Despite their intensive nature, most population management programmes have been underperforming and are unsustainable in the long term (Chargé et al. 2014; Lees and Wilcken 2009).

Currently, most breeding protocols use pedigree analyses to select suitable breeding pairs, aimed at retaining genetic diversity and reducing inbreeding (Asa et al. 2011; Chargé et al. 2014). The decision on who breeds with whom relies on decisions made by population managers and not on the individual animals or their mate preferences (Abts et al. 2018; Asa et al. 2011; Martin-Wintle et al. 2015; Martin-Wintle et al. 2019). This lack of choice may result in pair incompatibility, expressed by a lack of willingness to breed, failure to produce or raise offspring or even agonistic behaviours (Asa et al. 2011; Lees and Wilcken 2009; Roberts and Gosling 2004). These issues are frequently attributed to the absence of mate

choice and regarded as a key factor contributing to the failure of ex-situ population management programmes (Conway 2011; Martin and Shepherdson 2012; Wedekind 2002). Improving mate compatibility to increase reproductive success is regarded as particularly important for the long-term sustainability of population management programmes in zoos (Martin-Wintle et al. 2017).

Providing mate choice opportunities has been proven to increase fecundity, offspring survival and animal welfare (Asa et al. 2011; Drazan et al. 2025; Martin-Wintle et al. 2015; Martin and Shepherdson 2012; Roth 2026; Wedekind 2002) in many species in zoo population management programmes (Hartnett et al. 2018; Martin-Wintle et al. 2017; Martin and Shepherdson 2012; Parrott et al. 2019). For instance, Drazan et al. (2025) describe an increased efficiency of breeding within their marmoset colony by allowing females to choose their mate.

Furthermore, studies with a wide range of taxa have highlighted a variety of factors that drive mate choice, such as age (Abts et al. 2018; Brandies et al. 2018; Mainguy et al. 2008; Martín and López 2013), personality (Martin-Wintle et al. 2017), familiarity (Fisher et al. 2003; Martin and Shepherdson 2012; Roberts and Gosling 2004; Tang-Martinez et al. 1993), and genetic distance (Mossotti et al. 2018). Other factors, such as ontogeny (Bölting 2018; Ruploh et al. 2013; Sachser et al. 1994; Sachser et al. 2018), enclosure design and husbandry practices (Arumugam et al. 2020; Mellen 1991) might also influence mating behaviours and mate compatibility.

#### **Male aggressive behaviour in okapi**

A recurrent manifestation of pair incompatibility is the display of aggression among the members of the pair (Yamada and Durrant 1989; Zhang et al. 2004), which in extreme situations may lead to severe injuries or fatalities. In the EAZA Ex situ Programme (EEP) for okapi *Okapia johnstoni*, there are regular reports of aggressive behaviour being displayed during breeding introductions. In these occurrences, the male reacts aggressively toward the female, kicking and stomping her. This behaviour requires immediate action from the animal keepers and full separation of the animals to prevent fatal injuries to the female. It can be assumed that the occurrence of these aggressive episodes slows down and lowers the efficiency of the population management programme - the pair takes longer to achieve a pregnancy or fails to do so. Furthermore, in cases of extremely aggressive males, these have to be sent out again and exchanged for a new male, a process that takes valuable resources and time for the programme (Asa et al. 2011). Some okapi pairs, and especially some males, have been very difficult to breed, undermining their genetic representation and contribution to the population.

#### **Okapi husbandry practices**

The okapi is a large, endangered ruminant from Central Africa. Due to its elusive nature and remote habitat, very little is known about the behaviour of this species (Lindsey et al. 1999). Okapis in the wild usually live solitary, and males and females only meet to mate, spending very little time together. Males keep and protect larger territories than females, overlapping the home range of multiple females, presumably to have access to multiple partners (Hart and Hart 1988). Okapi females and their offspring may live nearby until the juvenile establishes its home range (Bodmer and Rabb 1992; Hart and Hart 1988; Lindsey et al. 1999).

In zoos, the most common group composition of okapi is a breeding pair, limiting the mate options available to each animal. However, some facilities are capable of housing more animals. In either situation, the enclosure design is composed of separate enclosures for males and females, so both can stay apart as would be expected in nature. Traditionally, the two individuals

are only introduced for breeding when the female enters oestrus. Nevertheless, some institutions allow the introduction of the male to the female nearly every day, including when the female is not in oestrus (=anoestrus). Some olfactory and visual communication can be accomplished through the barrier, but for many species, having access to scent marks and physical interaction is essential to exchange important information regarding individual identification, age or reproductive status, and it influences mate choice and breeding behaviour (López et al. 2003; Martín and López 2013; Parrott et al. 2007; Parrott et al. 2019). Whether this difference in the management of the female oestrus may impact pair compatibility is unknown, but possibly these frequent introductions build up familiarity among the pair and reduce the incidence of aggression.

Another common practice with okapi is the isolation of the parturient female and subsequent offspring from the social group. This means that the calf usually does not engage with other individuals till late in its development. In some instances, the juvenile only meets new individuals when transferred to a new institution or is introduced to a breeding mate for the first time. Some institutions have been trying to pair the dam and calf with other adult okapi. Whether this early socialisation is important for the development or learning of social and breeding behaviours in okapi is completely unknown. Adolescence has been increasingly described as a crucial developmental stage for the plasticity and shape of behaviour during adulthood, in which the social environment plays its role (Bölting 2018; Ruploh et al. 2013; Sachser et al. 1994; Sachser et al. 2018). Although generally solitary, okapi in the wild might have a more complex social life than assumed. While males patrol their territories, they might come across females with calves and temporarily interact. Encounters between females in adjacent home ranges may also occur. Hypothetically, such encounters, although short, can be relevant for the development and socialisation of young okapi.

This study aims to identify factors that influence okapi pair compatibility. Specifically, we examined which variables are associated with the occurrence of male aggressive behaviour during breeding introductions. The factors included were the age difference between the pair members; whether the pair was only introduced during the female's oestrus period or also regularly at other times (hereafter referred to as "oestrus husbandry"); enclosure design, more specifically the possibility for visual and physical contact through the fencing; and the individuals' socialisation prior to reaching breeding age. Additionally, we assessed whether male aggressive behaviour tends to occur primarily during initial introductions or persists throughout the breeding history of the pair.

#### **Materials and methods**

##### **Data collection**

A survey was distributed to the 23 institutions in the EEP housing breeding pairs of okapi in January 2021. These breeding pairs not only included the current living animals but also all the breeding pairs of okapi that have existed in the EEP since 1985. Each institution received the list of pairs that were once housed at its facility and the list of calves born at its facility. The survey was directed to staff members most familiar with the history and husbandry of okapi at their institution. It included questions about pair-related variables, individual variables and aspects of husbandry and enclosure design. These variables included the frequency of male aggressive behaviour (rated from 0: never occurred to 4: occurred every introduction); the pattern of occurrence of aggression during the pair's breeding history (limited to initial introductions or occurring continuously during their breeding history); the type of oestrus husbandry used for the

pair (allowing introductions during anoestrus or not); whether the enclosure design allowed for visual or physical contact; and each animal's history of socialisation with conspecifics prior to breeding age.

After completing the survey, a short meeting with keepers was arranged to clarify questions, verify their answers, and obtain further information and details about specific animals, their history and the facilities, if required. Birth location and date were extracted from the studbook, and 'date of birth' was used to calculate the age difference between the male and the female.

### Statistical analysis

A binomial generalised linear mixed model (GLMM) was created to determine which variables contribute most to the occurrence of male aggressive behaviour using the package lme4 in R (R Core Team 2025). The age difference, oestrus husbandry and the socialisation of each individual were used as explanatory variables (fixed effects). The zoo where each pairing occurred and the ID of each animal were treated as random effects. The explanatory variables of physical and visual contact were excluded from the analysis because all institutions that answered the questionnaire stated that their enclosures allow visual and physical contact between the animals when they are separated. The variables oestrus husbandry and socialisation (of both sexes) were treated binarily.

Due to male aggressive behaviour being ranked from 0 to 4, the data set had an overabundance of zeros (no aggressive behaviours observed). Therefore, a hurdle model was used to first assess the probability of attaining the value 1, and second to model the probability of the non-zero values. The first hurdle analysed which variables influence the occurrence of aggressive behaviour (all data above 0 were transformed into 1, forming a dataset of occurrence/no occurrence). The second hurdle examined the frequency of aggressive behaviour, using only the subset of observations where aggression occurred (i.e., those marked as 1 in the first hurdle). This was analysed with a linear mixed-effects model (LMM). The significance of fixed effects was assessed using Type III ANOVA tests (Wald  $\chi^2$ ) to evaluate their overall explanatory power. Each full model was compared with a null model that included only the random effects (and the intercept).

During the interviews with the keepers, many mentioned that pairs ranked as 4 were never introduced during the anoestrus period of the female because the level of conflict between the two individuals represented too much risk for the safety of the animals. This raises doubts about whether this variable explains the aggressive behaviour of the male or if it is the aggressive behaviour that defines the oestrus husbandry used for the animals. As such, the models were run, removing the pairs ranked as 4 ( $n=5$ ). Furthermore, because data for the socialisation of the animals (for both sexes) had some gaps, reducing the sampling

**Table 1.** Results of the General Linear Mixed Model (first and second hurdles) for the occurrence of male aggression. An ANOVA was performed for each hurdle to test the fitting of the data into the model.

|                                                                           |                       |      |       |          |
|---------------------------------------------------------------------------|-----------------------|------|-------|----------|
| Model: Age difference + Oestrus husbandry + Male and Female Socialisation |                       |      |       |          |
|                                                                           | First Hurdle (n=74)   |      |       |          |
|                                                                           | Estimate              | SE   | z     | Pr(> z ) |
| Age Difference                                                            | 0.04                  | 0.43 | 0.09  | 0.34     |
| Female Socialisation                                                      | -10.30                | 5.59 | -1.84 | 0.77     |
| Male Socialisation                                                        | 5.09                  | 5.0  | 1.02  | 0.31     |
| Oestrus Husbandry                                                         | -19.25                | 6.09 | -3.16 | <0.01**  |
| ANOVA                                                                     | Pr(>Chisq): <0.01**   |      |       |          |
|                                                                           | Second Hurdle (n=20)  |      |       |          |
|                                                                           | Estimate              | SE   | t     | Pr(> t ) |
| Age Difference                                                            | -0.00                 | 0.01 | -0.33 | 0.74     |
| Female Socialisation                                                      | 0.17                  | 0.16 | 1.11  | 0.28     |
| Male Socialisation                                                        | -0.12                 | 0.32 | -0.37 | 0.72     |
| Oestrus Husbandry                                                         | -0.34                 | 0.17 | -2.04 | 0.048 *  |
| ANOVA                                                                     | Pr(>Chisq): 0.2831    |      |       |          |
| Model: Age difference + Oestrus husbandry                                 |                       |      |       |          |
|                                                                           | First Hurdle (n= 118) |      |       |          |
|                                                                           | Estimate              | SE   | z     | Pr(> z ) |
| Age Difference                                                            | -0.00                 | 0.04 | -0.01 | 0.99     |
| Oestrus Husbandry                                                         | -1.50                 | 0.70 | -2.13 | 0.03*    |
| ANOVA                                                                     | Pr(>Chisq): 0.045*    |      |       |          |
|                                                                           | Second Hurdle (n=34)  |      |       |          |
|                                                                           | Estimate              | SE   | t     | Pr(> t ) |
| Age Difference                                                            | -0.00                 | 0.01 | -0.06 | 0.95     |
| Oestrus Husbandry                                                         | -0.05                 | 0.23 | -0.21 | 0.84     |
| ANOVA                                                                     | Pr(>Chisq): 0.98      |      |       |          |

size due to incompleteness, we repeated the analysis without this fixed effect to evaluate the outcome with a more robust sample size.

To analyse the likelihood of aggressive behaviour being limited to the first introductions or being persistent across time, a Chi-Square Goodness of Fit Test was used. Here, the observed proportion of observations among the two categories (beginning and continuous) was compared with an expected proportion of the observations. The expected proportions assume that the likelihood of a pair displaying male aggressive behaviour only on their first breeding attempts or continuously throughout their breeding history was the same (0.5/0.5), suggesting that no factor is contributing to this difference among pairs. A significance level of 0.05 was used in all the statistical analyses.

## Results

Of the 23 institutions contacted, 21 (91.3%) completed the questionnaire. From a total of 118 pairs of okapi in the EEP, assessed via the questionnaire, 40 (34%) displayed male aggressive behaviour. However, only six pairs (5%) were reported as having always been aggressive at each introduction (Figure 1). These six pairs did not produce any offspring.

From the 118 pairs assessed, 60 (51%) were reported as introduced regularly during the female's anoestrus, while 58 (52 if pairs ranked as 4 are removed) were reported as only introduced when the female was in oestrus. These numbers reveal a near-equal division on which type of husbandry was chosen by the keepers. When looking at the proportions of pairs that displayed aggression, 18.3% of the pairs in "together during anoestrus" displayed aggressive behaviour. This proportion increases to 44.2% in "together only in oestrus" (Figure 2).

The first hurdle of the model revealed that the oestrus husbandry chosen for the pair had a significant effect on the occurrence of male aggression. In contrast, age difference and the socialisation status of either the male or the female showed no significant effects. The ANOVA test comparing the full model with its null counterpart was significant, indicating that the inclusion of these predictors improved the model's fit to the data (Table 1).

In the second hurdle, oestrus husbandry remained a significant predictor of the frequency of aggressive behaviour during breeding introductions. However, the comparison with the null model was

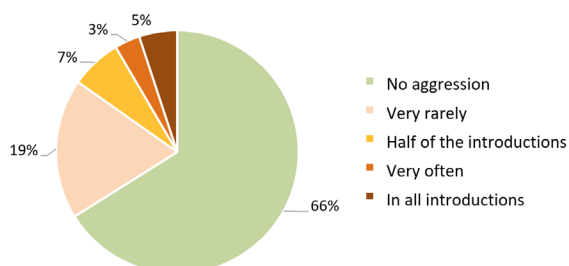


**Figure 1.** The proportion of okapi pairs that displayed aggression during breeding. The scores mean: 0: no aggression, 1: very rarely, 2: half of introductions, 3: frequently and 4: every introduction.

not significant, suggesting that the predictors in this hurdle did not collectively improve the model fit and do not explain the variability of the data (Table 1).

Note that, due to the occurrence of missing information in the socialisation of the males or the females, the model was run with only 74 of the 118 pairs assessed in the first hurdle and only 20 in the second hurdle. Removing socialisation as a fixed effect and yielding a larger sample size did not meaningfully change the outcome of the models (Table 1).

The Chi-squared test to see whether aggressive behaviour was more likely to occur only during the first introductions or to persist over time showed no significant difference between the two possibilities ( $\chi^2=1.4$ ,  $df=1$ ,  $P=0.24$ ), indicating that male aggression was about equally likely to occur during the initial introductions or to continue across the pair's history.

## Discussion

The results of our study clearly indicate that the oestrus husbandry chosen for each pair influences the likelihood of aggressive behaviour occurring during mating attempts. Pairs that were allowed to interact regularly, regardless of the female's reproductive status, perform better during breeding introductions than pairs that are only together when the female is in oestrus. Zhang et al. (2004) similarly observed in giant pandas *Ailuropoda melanoleuca* that aggression during breeding decreased when females and males were allowed to rotate and exchange enclosures before the oestrus peak of the female. This corroborates the idea that promoting regular contact among individuals promotes familiarity and the exchange of important individual information, such as reproductive status. Scent-marking and olfactory cues are very important for mate choice and communication in many mammal species and play a role in familiarity (Rich and Hurst 1998; Roberts and Gosling 2004; Parrott et al. 2007; Parrott et al. 2019). Swaisgood et al. (2000) suggest that in giant pandas, giving access to oestrous females' odours prior to breeding introductions may reduce aggression from males and enhance breeding interest.

Likewise, for the okapi, it might be important for the male to regularly assess the reproductive status of the female (e.g. urine inspection) as it is for the female to inspect the scent marks of the male. In their natural habitat, okapi males have large territories that overlap the territory of multiple females, which they patrol

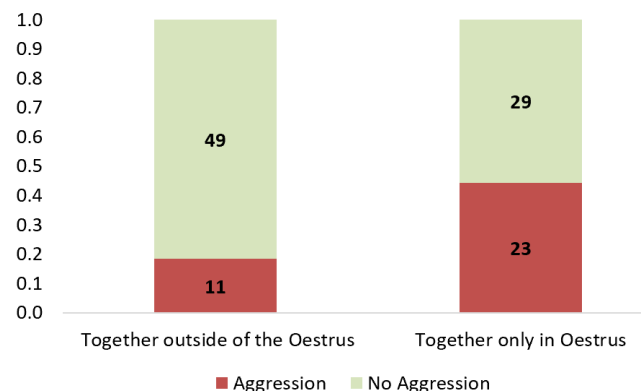


**Figure 2.** The proportion of pairs with and without the occurrence of male aggressive behaviour according to each type of oestrus husbandry. The number inside the bars represents the total number of pairs in each group. Pairs ranked as 4 (always aggressive) are not included.

and defend from rivals (Lindsey et al. 1999). Males may come across receptive females, staying in relative proximity, guarding the female while it is receptive or entering oestrus, and regularly meeting for courtship and mating. In zoos, however, the male does not have control over access to the female since this decision relies on the animal keepers. Although keepers are capable of determining the timing of the female's oestrus through visual and behavioural signs (from both the female and the male), their level of accuracy is limited (Meireles and Hofman 2024). As such, the female might already be finishing the oestrus when the male is introduced. It is conceivable that a male who detects a receptive female but does not have access to her will increasingly become frustrated and perhaps become too persistent when finally given access to the female. If the female does not show receptiveness towards this male, his behaviour might escalate towards aggression. Lack of control over their environment (in this case, access to a breeding partner), has been described as having a negative impact on animal welfare, especially in captive animals, where the environment has several restrictions (Markowitz and Aday 1998; Owen et al. 2005; Rust et al. 2024). Giving an okapi male regular access to the female might give him increased control over the environment by creating and extending the opportunities to choose to remain close to the female or to remain apart. Additionally, although all institutions reported that their facility design allows individuals to have permanent visual and physical contact through a barrier, this might still be too limited regarding the exchange of information and social interactions.

Although our results indicate an influence of the oestrus husbandry on the occurrence of aggressive behaviour, it is important to consider potential confounding factors. As described before, the decision to allow the members of the pair access to one another does not rely on the animals but instead on their keepers. As such, human bias cannot entirely be ruled out as driving the results observed in this study. It can be expected that keepers are reluctant to introduce pairs that they perceive as being incompatible due to the dangerous implications of separating two large animals. Therefore, the choice to either introduce them more often (when the female is anoestrous) or only try when the female is receptive (in oestrus) may be strongly influenced by the keepers' perception of compatibility. Similarly, when the pair behaves harmoniously, it may incentivise the keepers to introduce them regularly. During the interviews, some keepers mentioned a strong apprehension about pairing animals again after a first pairing attempt resulted in an extremely aggressive response from the male. We therefore decided to remove these pairs from our analyses since, in these particular situations, we believe that the oestrus husbandry was determined by the occurrence of aggression and not the other way around. If the same happened to a certain degree with the other pairs where aggression occurred (ranks 1 to 3) is unclear. The same human-driven decision happens in the giant panda population management programme, as the animals are only allowed to mate if the keepers perceive their behavioural interactions as positive (Zhang et al. 2004). Human bias was also suggested as a potential confounding factor in a study on the link between familiarity and pair success in koalas *Phascolarctos cinereus* (Brandies et al. 2018).

Given that in our dataset breeding introductions with aggression were equally likely to be restricted to the initial introductions or to persist through the breeding history of a pair, this seems to exclude the potential role of familiarity or learning through repetitive and consecutive breeding introductions. A potential explanation might be that some females may learn that the male is aggressive in the first attempt and always behave less receptively to that male in following introductions, killing the chances for familiarity to build up and leading to a continuous lack of compatibility. From a population manager's perspective, this suggests that when facing

a problematic pair, the chances that the situation will improve are limited, and the decision on whether to keep trying or swap the animals must be made on a case-by-case basis.

Our results did not indicate the age difference as a factor leading to aggressive behaviour during mating. Several studies on koalas in a population management programme (Bercovitch et al. 2006; Abts et al. 2018; Brandies et al. 2018) found effects for both the age difference and the absolute age of either the male or the female of the pair. These effects were associated with female reproductive health, the breeding system and male fitness. For instance, all studies found higher copulation success when pairing a male older than a female. Although it seems that age difference does not play a role in the mating success of okapi, it would still be relevant to further investigate the effects of the age of each individual at a given pairing attempt, as mating success and breeding behaviour might change between age classes or be sex-dependent. For instance, Brandies et al. (2018), found that the age of the female in koalas was not significant for copulation success, while the age of the male did play a significant role. In our study, it was not possible to obtain the absolute age of each individual at a given pairing attempt, so we were not able to tell whether mating success differs between young and mature okapi males.

No statistically significant effect of the socialisation of young okapi was found within our data. However, some keepers described individual okapis that were highly socialised when young as being very calm and easy to introduce to other individuals, which also resulted in individuals that were easy to breed. Some studies in birds and rodents point out that the social environment during ontogeny influences adult behaviour during breeding (Sachser et al. 1994; Ruploh et al. 2013; Bölting 2018). Price and Stoinski (2007) also point out that the social housing of zoo mammals has an impact on reproductive success and individual welfare, with various results depending on the species, group sizes and structure.

Although no effect could be observed regarding socialisation and mating success in okapi, we argue that creating a more enriching and complex social environment for both young and adults brings other benefits. The captive environment is, in general, poorer in stimuli compared to the wild environment. As such, increasing the social complexity of the social group can provide extra stimuli and new behavioural opportunities to zoo-housed animals. Prince and Stoinski also indicate that even species that are usually solitary in the wild show increasing positive aspects when housed in more complex social structures in zoos. A remarkable example of that is the orangutans (*Pongo* sp.), which are solitary rainforest dwellers. In zoos, they show high social interactions, increased breeding success and positive welfare when housed in groups. However, the opposite can also occur as described for some felid species (Price and Stoinski 2007). In okapi, usually considered a solitary species, social interaction between individuals in zoos is generally regarded as positive, with the individuals performing allogrooming, greetings and even play behaviour, which might indicate some flexibility as observed in orangutans. As such, we believe that for okapi, offering the individuals plenty of opportunities to meet and interact will increase their welfare and facilitate introductions even if this does not translate into increased mating success.

## Conclusions

The okapi EEP, despite the issues highlighted in this study, is quite successful in breeding its animals and increasing its population size. However, nearly one-third of pairs with reported cases of male aggression represent one phenomenon that a population manager or the holding institutions cannot ignore. These cases lower the efficiency of breeding and increase the logistics of the programme. The results of this study point out that some

husbandry practices can play a role in the occurrence of male aggression, most notably the oestrus husbandry. More pairs that were allowed to be together regardless of the oestrus status of the female were reported as not having issues with male aggressiveness.

We recognise that, given our low sample size, no stronger conclusions can be drawn; however, we expect that in future, more data might be available for a more robust analysis, and we welcome the inclusion of other components, such as behavioural and hormonal analysis. This further research will be essential to more deeply understand the mechanisms related to pair compatibility in okapi, including the role of oestrus husbandry suggested by us, since a human bias can be behind the results described here.

Lastly, although the socialisation of the young okapi did not stand out as playing a role, we still argue that providing a more complex and enriching social environment to the animals, either young or adult, brings welfare benefits which ultimately reflect on breeding success.

This study collated information which had already been noted at individual zoos holding okapi and interviews with experts working with the species as part of an EAZA EEP; thus, its ethical ramifications had been considered at both an institutional and regional level and classified as low-risk, so it was not reviewed by a full ethics committee.

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