

Current social management practices contribute to reproductive failure in zoo-housed guenons

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Abstract

Recent emphasis on reflecting natural behaviour and wild group composition in zoo-housed social animals has resulted in substantial improvement in captive breeding and welfare. We investigated studbook data for four guenon species housed in European zoos to assess the role of zoo management practices in the reproductive success of social species. We hypothesized that group dynamics reflecting wild living, including early social experience, would be associated with greater reproductive success. Our findings are presented in a standardized qualitative risk assessment with an additional certainty measure in the form of literature evidence. We found that greater reproductive success was associated with more potential breeding partners in L'Hoest's, Roloway and Diana monkeys and with larger group sizes in all species studied here, providing support that mimicking wild group size, composition, and dynamics under captive conditions can improve reproductive success. Unexpectedly, greater reproductive success was associated with earlier first inter-facility transfers in female L'Hoest's and Diana monkeys, and with more frequent inter-facility transfers in male L'Hoest's and Diana monkeys. Furthermore, for male Diana monkeys and female and male L'Hoest's monkeys, mothers with less reproductive and rearing experience tended to produce offspring that in turn had greater reproductive success, hinting at more complex and sex-differentiated mechanisms underlying sub-optimal reproduction in zoo guenons. Our findings highlight the importance of carrying out species-specific studies, and demonstrate that zoo management and husbandry practices can inadvertently impact reproductive success. We recommend that zoos holding guenons consider reducing the number of guenon species they hold in favour of increasing group size to improve reproductive success.

Keywords

Cercopithecus, management, conservation breeding program, social behavior

Introduction

Breeding animals in captivity is becoming increasingly important as many species are rapidly declining due to anthropogenic impacts. Zoos play an important role in conservation by safeguarding endangered species with the aim of subsequent reintroduction or supplementation of wild populations (Leus, 2011). However, species recovery requires sustainable and demographically balanced captive populations that have high genetic diversity. Establishing such populations has been successful in only few primate species (e.g. Kaumanns et al. 2020; Gibson and McCann, 2013). By far the most successful species recovery is that of the golden lion tamarins (GLT) (*Leontopithecus rosalia*). These primates almost became extinct before the early 1980s when the GLT Conservation Programme was initiated (Kierulff et al., 2012). Zoos played a substantial role in the successful recovery of this species by establishing a self-sustaining captive population of GLTs and contributing most of the individuals for reintroductions (Kierulff et al., 2012). Through the combined effort of *ex-situ* and *in-situ* conservation, GLT numbers in the wild have increased and the International Union for Conservation of Nature (IUCN) Red list status changed from Critically Endangered to Endangered (Kierulff et al., 2012).

However, many conservation breeding programs demonstrate low breeding success (Martin-Wintle et al., 2015), some of which stem from inadequate management practices. For instance, captive lion-tailed macaque (*Macaca silenus*) populations have experienced drastic declines due to logistical issues and subsequent contraceptive measures; the North-American subpopulation has almost entirely been reduced to non-breeding stock (Begum et al., 2022). Likewise, the captive Goeldi's monkey (*Callimico goeldii*) population has experienced poor reproductive success due to poor understanding of the reversibility of contraceptive implants used for this population (Gibson and McCann, 2013). In other species, the reasons behind sub-optimal reproduction in captivity remain undetermined. For instance, mated pairs of captive Diana monkeys (*Cercopithecus diana*) continuously fail to produce offspring (Gibson and McCann, 2013).

Although having a demographically balanced and genetically robust founder population is essential for successful conservation breeding programs, success depends on other major contributing factors, such as species-specific reproduction requirements, social management and appropriate husbandry practices, including visitor presence and visitor-animal interaction (e.g. Young, 1998; Williams et al. 2022). Zoo animals experience a fundamentally different physical environment compared to their wild-living counterparts (Wormell and Price, 2018). However, their social environment is equally important. For instance, previous primate studies demonstrate that early inter-facility transfers and a lack of juvenile social and allocare opportunities can result in the failure to navigate through the dominance rank system (Pereira and Leigh, 2003; Förster and Cords, 2005; Heintz et al., 2017), failure to acquire adult roles (Förster and Cords, 2005), poor parenting skills (Ross and MacLarnon, 2000; Cleveland et al., 2004; Silk et al., 2009; Sproul Bassett et al., 2020) and overall poor reproductive success (Price, 1992; Kuhar et al., 2003). Suboptimal group size can also directly affect reproductive success (Kuhar et al., 2003; Leong et al., 2004; Nuss and Warneke, 2009). For instance, in communally rearing primates such as cotton-top tamarins (*Saguinus oedipus*), a small captive group size can result in a lack of rearing helpers which ultimately leads to high offspring mortality (Leong et al., 2004).

Social factors have now been recognized as crucial factors which influence the reproductive success of several species in captive environments. In particular, the lack of mate choice (Bluhm and Gowaty, 2004; ASA et al., 2011; Martin-Wintle et al., 2015; Schulte-Hostedde and Mastromonaco, 2015; Hartnett et al., 2018), lack of allocare and maternal experience (Stanley and Hartley, 2016), and changes to social groups (Williams et al., 2020) have been indicated as factors contributing to the lack of reproductive success in a wide range of taxa. These studies show that improving social management practices can enhance the reproductive success of captive animals.

Most primates are group-living animals with a complex social organization that is difficult to mimic in captive conditions; this likely contributes to the lack of breeding success in captivity (Price and Stoinski, 2007; Gillman et al., 2017). One such group of primates experiencing low reproductive

success in captivity are guenons (*Cercopithecus* spp.), a diverse group of African monkeys. Guenons in the wild live in close female-bonded groups where females are philopatric and males disperse from their natal group upon reaching maturation (Butynski, 2002). With more guenon species becoming listed as vulnerable or endangered on the International Union for Conservation of Nature (IUCN) Red List, the need for conservation actions for these species is critical (IUCN, 2022). As of 2021, European Association of Zoo and Aquaria (EAZA) *ex-situ* programs (EEP) exist for five species of guenons: De Brazza's monkey (*Cercopithecus neglectus*), Diana monkey (*Cercopithecus diana*), Roloway monkey (*Cercopithecus roloway*), L'Hoest's monkey (*Cercopithecus lhoesti*) and Hamlyn's monkey (*Cercopithecus hamlyni*). These species live in groups of two to 38 in the wild. Specifically, *C. neglectus* live in groups of two to 10, averaging 6.6 individuals in the wild (Mugambi et al., 1997), while reported group sizes for *C. roloway* range between 12 to 15 individuals (Curtin, 2002, Gonedelé Bi et al., 2013). *C. diana* groups in the wild range from 20 to 30 individuals (Uster & Zuberbühler, 2001). Reports of group sizes for *C. hamlyni* tend to differ, with studies reporting smaller group sizes of two to three individuals (Hall et al., 2003) and 3.6 individuals on average (Easton et al., 2011), while other studies note relatively larger group sizes (up to ten individuals reported by Kingdon (2015) and a minimum of 22 individuals reported by Easton et al. (2011)). *C. lhoesti* was found in relatively larger groups averaging from 10 to 17 individuals (Ukizintambara, et al., 2019) and even up to 38 individuals in a study by Tashiro (2006). However, despite the efforts to provide a suitable environment, the overall reproductive success is poor and births in most captive guenon species are rare.

Aims and hypothesis

Here, we investigated the specific components of the social life of captive guenons in European zoos to identify factors that were associated with sub-optimal reproduction. We focused on the following social factors and their potential association with poor reproductive success: (1) early social life experience (the age at first inter-facility transfer, social experience with siblings), (2) number of potential partners, (3) group size, (4) reproductive experience of the mother (the number of offspring

the mother had given birth to during her lifetime), and (5) successful rearing experience (successfully rearing own offspring to >1 year of age, allocare, and experience of other female's birth).

These potential risk factors for poor reproductive success were assessed by analyzing European zoo studbooks for four different species of guenons: Diana monkey (*C. diana*), Roloway monkey (*C. roloway*), L'Hoest's monkey (*C. lhoesti*), and Hamlyn's monkey (*C. hamlyni*). De Brazza's monkeys were not included in this study because their captive breeding program differs considerably from the other guenons in European zoos. De Brazza's monkeys have to be managed with limited breeding, and a large number of animals are contracepted due to space restrictions, resulting in differing breeding opportunities between individuals. In contrast, the breeding recommendations for *C. diana*, *C. roloway*, *C. lhoesti*, *C. hamlyni* allow for a unique opportunity to investigate the breeding factors in captivity, as due to their poor reproductive success, all except medically unfit individuals are recommended for breeding.

Methods

Investigation of social factors

We investigated risk factors in the following species of guenons: *C. diana*, *C. lhoesti*, *C. roloway*, and *C. hamlyni*. The EAZA EEP Co-ordinators for all four species of guenons were consulted and approved this study. The Guenon Subgroup Leader within the Afro-Eurasian Primate Taxon Advisory Group, Dr Hartley, is a co-author of this paper and provided his input on the applicability of this research towards EEP efforts.

We used Zoological Information Management Software (ZIMS) to extract studbook datasets and transactional, behavioural and other notes on all four species of guenons (downloaded on 23rd February 2021 and supplemented this with live information throughout the study period) which were or are currently held in European zoos. The datasets date back to the first appearance of guenons in European zoos and encompass all individuals between 1979 and 2021 (Table 1). Using ZIMS, we

excluded females which had medical conditions that would make them undesirable to breed, such as diabetes. The data were then used to generate family trees and timelines, which allowed us to obtain values for each variable. Both numerical and binary social risk factors for poor reproductive success were investigated (Table 2).

Although there is some variation in the housing and zookeeping conditions across the European zoos, our research focuses on factors that can be managed by studbook coordinators and that are recorded in studbooks. This consisted of group size, age of transfer out of maternal group, number of potential partners, housing with other animals with rearing experience, number of siblings individuals experience, individuals maternal experience.

Risk Assessment Design

Individual social risk factors for zoo-housed guenons were assessed using a risk management process (Hartley, 2016). Such method allowed us to estimate which identified factors pose the greatest risk to reproductive success and was successfully used in a study by Hartley (2016) which resulted in the refinement of husbandry practices to improve welfare and reproductive success in captive elephants (*Elephas maximus*, *Loxodonta Africana*) (Hartley and Stanley, 2016). In addition, this format allows us to indicate any uncertainty linked to our data source. Studbook data analysis can aid in detecting how specific social management practices affect reproductive success. However, results of such analysis are substantially limited by small sample sizes and missing data (Sackett et al., 2010). To accommodate these limitations, we provide an additional element of certainty within our qualitative risk assessment in the form of existing evidence from peer-reviewed literature.

We developed a risk pathway to indicate how social factors affect each step in the chain of events towards successful reproduction, starting with a sexually mature pair of guenons in the same enclosure and resulting in the successful rearing of an offspring (Fig. 1). In addition, some factors play roles in various steps across the risk pathway, indicating their complex and possibly multiplied effects on reproductive output.

We undertook a qualitative analysis of the identified social risk factors and their effects on the likelihood of sub-optimal reproduction in guenons by assigning a risk category based on studbook data evidence. Statistically significant results of the studbook data analysis result in high risk, and statistically non-significant results of studbook data analysis are denoted as low risk. We implemented a certainty measure to our risk assessment to recognize conflicting, absent, or insufficient information. High uncertainty denotes contradictory trends in the two sources of data, medium uncertainty indicates lack of information or limited information on the effect of the social factor on reproductive success in literature and low uncertainty indicates both sources of data support a similar risk assessment.

The literature review electronic search methodology

The literature review was undertaken to identify evidence for the impact of social factors at one or multiple locations in our risk pathway for sub-optimal reproduction. As publications on wild guenon species of interest here are limited, we used available literature on other species to make conclusions about our findings. A peer-reviewed literature search was aimed at topics relevant to our study area based on a range of keywords (see supplementary material, Table S1), searched within the following journal databases: Web of Science, Scopus and Science Direct. Furthermore, the reference lists of articles and search tool Connected Papers (www.connectedpapers.com) were utilised for identifying additional, prior, and derivative papers. Primarily, studies of Cercopithecinae were included with the addition of relevant studies linking reproductive success and social factors in other primates and mammals.

Statistical analysis

We conducted all statistical analysis in R software, version 3.6.1 (R Core Team, 2019) and the figures produced were created using the ggplot package (Wickham, 2016). The statistical significance level for all components of statistical analysis was set at $\alpha=0.05$. We analyzed each social factor separately

for males and females, as the life history and the reproductive role of each sex differs substantially (Butynski, 2002). Only guenons that have reached sexual maturity (>4 years old) were considered within our analysis of the impact of social factors on reproduction. Furthermore, if males remained in their natal group at an age greater than four years, they were not considered as breeding males due to potential reproductive suppression.

Analysis of numerical social factors

We divided our data into two groups: breeders (individuals that have reproduced) and non-breeders (individuals that have failed to reproduce). To assess whether there is a statistical difference for each numerical risk factor, we tested these two groups of unpaired data. For normally distributed data, we used an unpaired t-test. For non-normally distributed data, we attempted data transformation to normalize data distribution. When transformation was not possible, we used a non-parametric equivalent of the unpaired t-test, Mann-Whitney U test. Means and standard deviations were back-transformed for the results section to provide a clearer interpretation (Lee, 2020).

Analysis of binary social factors

We used Chi-square test of Independence for the investigation of the association between binary social factors and breeder/non-breeder groups to determine whether there is a significant relationship between reproductive success and experiencing allocare, siblings and birth in group.

Results

Statistical analysis

Overall, 30-50% of all sexually mature individuals which are housed or were housed in European zoos have failed to reproduce (*C. diana*: 38%, (breeders: n=32; non-breeders: n=19); *C. hamlyni*: 31% (breeders: n=34; non-breeders: n=15; *C. roloway*: 53% (breeders: n=25; non-breeders: n=28; *C. lhoesti*: 46% (breeders: n=42; non-breeders=36). According to the analysis of the studbook data the

dam's age at first reproduction (in years) in European captive guenons averaged: *C. diana* 7.7 (SD= 3.7); *C. hamlyni*: 6.6 (SD= 2.5); *C. roloway*:8.0 (SD= 1.9) and *C.lhoesti*: 6.6 (SD= 2.5).

L'Hoest's monkey (females)

Reproductive success in female *C. lhoesti* housed in European zoos was greater in individuals that were significantly younger when first transferred between facilities, (Table 3, Fig.2a) and had a higher number of potential partners (Table 3, Fig.2b), and a larger maximum group size (Table 3, Fig.2c). The maternal experience was also associated with reproductive success in female *C. lhoesti* in captivity; daughters of mothers that produced fewer offspring (Table 3, Fig.2d) and successfully raised fewer offspring beyond a year old (Table 3, Fig.2e) had greater reproductive success.

L'Hoest's monkey (males)

Reproductive success in male *C. lhoesti* housed in European zoos was greater in males that experienced a higher number of inter-facility transfers (Table 4, Fig.3a), and had a higher number of potential partners (Table 4, Fig.3b). Similarly to captive female L'Hoest's monkeys, the maternal experience had the same effect on the reproductive success of the captive male L'Hoest's monkeys: greater reproductive success was associated with sons of mothers that produced fewer offspring (Table 4, Fig.3c) and successfully raised fewer offspring beyond a year old (Table 4, Fig.3d).

Roloway monkey (females)

None of the social factors showed trends associated with the reproductive success in female *C. roloway* housed in European zoos (see supplementary material, Table S2).

Roloway monkey (males)

The reproductive success was significantly greater in male *C. roloway* housed in European zoos that experienced a higher number of potential partners (Table 5, Fig.4a) and a larger maximum group size (Table 5, Fig.4b).

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256 *Hamlyn's monkey (females)*

257 Greater reproductive success in female *C. hamlyni* housed in European zoos was found in individuals
258 that had a larger maximum group size (Table 6, Fig.5a). Maternal experience also influenced the
259 reproductive success in captive female Hamlyn's monkeys: daughters of mothers that produced a
260 greater number of offspring (Table 6, Fig.5b) and successfully raised more offspring beyond one year
261 of age (Table 6, Fig.5c) showed greater reproductive success.

262

263 *Hamlyn's monkey (males)*

264 None of the factors showed trends associated with reproductive success in male *C. hamlyni* housed in
265 European zoos (see supplementary material, Table S3).

266

267 *Diana monkey (females)*

268 Reproductive success in female *C. diana* housed in European zoos was greater in individuals that
269 experienced their first inter-facility transfer earlier in their mature life (Table 7, Fig.6a), had a higher
270 number of potential partners (Table 7, Fig.6b) and a greater minimum and maximum group size
271 (Table 7, Fig.6c and 6d). Additionally, captive female Diana monkeys that experienced another
272 female giving birth also had greater reproductive success (Table 7, Fig.6e)

273

274 *Diana monkey (males)*

275 Male *C. diana* housed in European zoos that had greater reproductive success experienced a higher
276 number of inter-facility transfers (Table 8, Fig.7a) and a larger maximum group size (Table 8, Fig.7b).
277 Moreover, reproductive success was greater in sons of mothers that produced fewer offspring (Table
278 8, Fig.7c) and successfully reared fewer offspring beyond one year of age (Table 8, Fig.7d)

279

280 Overall, our results support the hypotheses about the importance of multiple potential breeding
281 partners and a larger group size for greater reproductive success. Our hypothesis about the association

between sub-optimal reproduction and the early age at first inter-facility transfer was not supported, and we found that transfers of young Diana and L’Hoest’s females soon after their sexual maturation were associated with reproductive success. Furthermore, greater reproductive and rearing experience of the mother was associated with increased reproductive success in her offspring only in female Hamlyn’s monkeys and the opposite trend was found in female Diana monkeys and male and female L’Hoest’s monkeys. Experiencing another female giving birth had a positive effect on reproductive success only in Diana female monkeys, whereas the other investigated factors (age of dam, allocare and sibling experience) showed no association with reproductive success in any guenon species. Tables 9-12 show the results of the risk assessment analysis and indicate which factors pose high/low risk and the certainty of our assessment. The risk factors and their impacts on the studied populations of guenons are summarised in Table 13 along with our proposed mitigating actions and future research directions.

Discussion

Overall, we found that a low number of potential breeding partners posed a high risk to reproductive success in female and male L’Hoest’s monkeys, male Roloway monkeys and female Diana monkeys (Table 13). Similarly, recent papers highlight that the preclusion of mate choice can result in unsuccessful mating and lower reproductive success of the offspring, and thus have adverse effects on the success of conservation breeding programs (Neff and Pitcher, 2005; Martin-Wintle et al., 2015; Schulte-Hostedde and Mastromonaco, 2015; Hartnett et al., 2018). A study on wild patas monkeys (*Erythrocebus patas*) investigated female choice by analysing the rate at which females solicited mating during the mating period (Chism and Rogers, 2010). This study found that not all available males were solicited; females showed a preference for certain males and avoided others for reasons as yet unidentified. However, the female choice did not affect copulation rates, and the authors argue that the solicitations by females could instead be associated with female-female competition and ensuring that a chosen male mates with her at the peak of her ovulation period. In addition to female

choice, our results indicate that male choice also plays a role in reproductive success of L’Hoest’s and Roloway monkeys. Similar results were found in other captive populations, including giant pandas (*Ailuropoda melanoleuca*) (Martin-Wintle et al., 2015). We suggest that allowing animals the choice to select a compatible mate could considerably increase the chances of reproductive success. This method is novel for conservation breeding programs but has shown great success in several captive mammal species (Martin and Shepherdson, 2012; Martin-Wintle et al., 2015; Hartnett et al., 2018).

Despite several studies demonstrating that social instability within zoos can result in social hierarchy breakdown and higher aggression (e.g. Beisner et al., 2015; Christensen et al., 2011; Williams et al., 2020), we found that successful breeding was linked to a higher number of inter-facility transfers in the European captive population of Diana monkeys and L’Hoest’s monkeys. However, this finding was only found in males. In the wild, males usually disperse from their natal group once they reach sexual maturity and continue migrating between social groups (Butynski, 2002). Our findings suggest that inter-facility transfers could mimic guenons’ wild dispersal patterns, which could enhance reproductive success (e.g. Epplé, 1978; Price and McGrew, 1990). This has also been demonstrated in captive cheetahs (*Acinonyx jubatus*), where Gillman et al. (2017) found that inter-facility transfers coinciding with natural dispersal pattern enhanced breeding success.

Another potential high risk to reproductive success was the age at first inter-facility transfer. We suspected that premature age at transfer may disrupt the guenon juvenile period and could later impact reproductive fitness. In primates, social experience during this time facilitates greater exposure to varied social interactions and enables the acquisition of skills important for orienting through the complex intricacies of primate social systems (Pereira and Leigh, 2003; Thompson, 2018). This was not the case for any guenon species investigated, as mean age at first inter-facility transfer across all zoos investigated was well above the age at which guenons reach sexual maturity; our findings indicate appropriate zoo management practices in terms of transfer timing for the four guenon species living in European zoos. Conversely, we found that transferring female L’Hoest and Diana monkeys shortly after reaching sexual maturity (around four years of age) was associated with greater

reproductive success, and staying in their natal group beyond this age was associated with reduced reproductive success. Guenons are generally described to live in a one-male social system where a dominant male resides in a group of philopatric females (Butynski, 2002). Male dispersal upon reaching sexual maturity is a common mechanism in guenons while female social dispersal is uncommon. Yet, our findings suggest that young L'Hoest and Diana females can successfully reproduce even when transferred from their natal group into a new social group.

However, the social behaviour of primates is flexible and is largely driven by local conditions (Isbell and Young, 2002). For example, some guenons, such as *C. hamlyni* or *C. neglectus* live in groups averaging 6.6 individuals in the wild (Mugambi et al., 1997), thus female dispersal may outweigh the benefits of staying in the natal female group. Retaining such a mechanism in captivity could mitigate the potential adverse effects of early interfacility transfers by allowing captive guenons to cope well with frequent transfers and to bond with new group members at an early age. It is also important to note that the conditions under which these artificial migrating events take place are controlled, closely supervised and often involve multiple steps of introducing a new member to an existing group (Hartley and Chapman, 2018). These conditions widely differ from a natural female dispersal event as they increase the likelihood of successful introduction into an established group. This might contribute to the lack of impacts of inter-facility transfers on reproductive success of young females found in our study.

We also found that larger group size was an important predictor of greater reproductive success in all four species investigated, yet for *C. lhoesti* and *C. diana* the average maximum and minimum group sizes were considerably smaller than in their wild counterparts. Similarly, *C. roloway* in our study had a smaller maximum group size compared to wild groups. Such large group sizes are difficult to mimic in captive settings largely due to space restrictions. *C. hamlyni* was the only species we examined that had similar captive and wild group sizes, which were comparably a lot smaller than for the other species investigated. Our findings indicate that a small group size could contribute to poor breeding success seen in European zoo-housed guenons, as several studies on captive species show that

inappropriate group size is associated with sub-optimal reproduction, abnormal behaviour, aggression, and social incompetency (Leong et al., 2004; Scott et al., 2017; Neal Webb et al., 2019). However, the association between reproductive success and larger group size should be interpreted with caution as successfully breeding individuals are inherently linked to larger group sizes due to the presence of their offspring. Despite this, we suggest that zoos consider increasing guenon group size to allow for increased mate choice and more appropriately mimic wild group composition. Given housing constraints, it may be more appropriate for zoos to reduce the number of guenon species they hold, and instead focus on larger groups of one or two guenon species.

We expected that allocare and experiencing other group members giving birth would be associated with greater reproductive success, as these social factors can contribute to the acquisition of parenting and social skills (Fairbanks, 1996; Chism, 2000; Ross and MacLarnon, 2000). With the help of allocarers, the mother can spend more time foraging (Fairbanks, 1990), wean their offspring earlier which facilitates a shorter inter-birth interval, and allows the offspring to mature quicker and start breeding (Chism, 2000; Ross and MacLarnon, 2000). Allocarers gain critical maternal experience and strengthen their social bonds which can help them develop alliances and acquire social support in within- and between-group conflicts (Chism, 2000; Ross and MacLarnon, 2000; Förster and Cords, 2005). Our study did not indicate that these factors were important predictors of reproductive success in the four species of captive guenons, except for female Diana monkeys, where gaining experience from other group members giving birth was associated with higher reproductive success. It is likely that the costs of allocare (e.g. energy investment of allocarers and offspring maltreatment) outweigh its benefits in captive settings.

It is generally assumed that increasing parity, and thus reproductive and rearing experience, improves the behavioural care and physiological investment in the offspring, which is in line with our findings for female Hamlyn's monkeys (Hinde et al., 2015; Nuñez et al., 2015). However, we also demonstrated a significant association between greater maternal experience and lower reproductive success in captive male Diana monkey and male and female L'Hoest's monkeys. Similar unexpected

results were seen in a study of rhesus macaques (*Macacca mulatta*) in which first-born individuals showed better three-year survival probability compared to later-born individuals (Nuñez et al., 2015). Although this study considered survival rather than reproduction, the overall fitness of the offspring is a strong predictor for reproductive success. The authors argue that this could be due to inexperienced mothers being more defensive and restrictive of their infant behavioural activity, which can result in more energy being available to the infant's growth and hence better overall fitness. This combined with relaxed ecological constraints in captive settings (i.e. predator-free and food-rich environment) could explain our findings.

The studbook data used in this study allowed for the first large-scale study of European zoo guenons, enabling us to identify the risk factors for their reproductive rates. Studbook data provide multi-generational information which is invaluable for investigating long-term patterns of sub-optimal reproduction. However, certain parameters are not included in the studbook database, such as information about enclosures and causes of death in juveniles and newborns. This information would aid in distinguishing between social management contributions to low reproductive success and patterns which naturally occur in primates.

Conclusion

This is the first studbook-based study on guenons held in European zoos and is the first to assess the impacts of social management on the reproduction of guenons in captivity. Our findings are presented in a qualitative risk assessment, which provides evidence-based predictions and allows a full transparency of uncertainty. Given that larger group size was associated with improved reproductive success in all species studied, and that space constraints often prevent holding large groups, we strongly recommend that zoos holding guenons consider reducing the number of guenon species they hold in favour of increasing group size of a single guenon species to improve reproductive success. We also recommend for future research to include a questionnaire-based study to collect data focusing

on individual birth events across zoos. This would aid in assessing the impacts of specific housing and group conditions, as well as previous medical and reproductive history.

Acknowledgements and Ethical Statement

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Tables

Table 1: For *Cercopithecus roloway*, *C. diana*, *C. hamlyni*, and *C. lhoesti*, the entire European population since the first recorded breeding occurred in European zoos were included in the analysis. The current numbers in European Zoos are 36 *C. roloway* (16 males, 20 females across 13 zoos), 70 *C. diana* (30 males, 36 females, 4 undetermined across 18 zoos), 22 *C. hamlyni* (10 males, 11 females, and 1 undetermined across 8 zoos), and 66 *C. lhoesti* (27 males, 37 females, 2 undetermined across 16 zoos).

Species	Start date of Records	Total Number of Animals included	Males	Females	Undetermined	Holding Zoos
Roloway Monkey	1977	75	39	36	0	17
L'Hoest's Monkey	1986	207	122	63	22	14
Diana Monkey	1982	158	77	74	7	22
Hamlyn's Monkey	1982	68	27	32	9	10

Table 2: The numerical and binary variables used in this study representing potential social risk factors for sub-optimal reproduction in guenons. The specifics for each variable are included to allow for full understanding of the criteria associated with each variable. The binary variables were investigated in the pre-sexual maturation period of each guenon (< 4 years of age).

Variables	Criteria	Tool used
Age at first inter-facility transfer (in months)	First transfer from a natal group to a different facility	Timelines
Number of transfers	Number of inter-facility transfers	Timelines
Number of potential partners	Included only guenons older than four years old. Excluding siblings, half-siblings, offspring, parents.	Timelines
Minimum group size	Excluding the natal group to which individuals were born into.	Timelines
Maximum group size		Timelines
Age of dam [†]		-
Reproductive experience	No. of offspring dam [†] has had	Family trees
Successful rearing experience	No. of offspring dam [†] has had which survived >1 year	Family trees and timelines
Unsuccessful rearing experience	No. of offspring dam [†] has had (died <1 year)	Family trees and timelines
Experienced sibling	Present in the same group as their sibling.	Timelines and family trees
Alloparenting	Present in the same group as both parents and their younger sibling for at least a year.	Timelines and family trees
Held in group with births	Present in a group in which birth took place, excluding sibling births.	Timelines and family trees

[†] Dam refers to the mother of the individual guenon being investigated

Table 3: The results of statistical analysis of the association between reproductive success and social factors for captive female L’Hoest’s monkeys. Mean value for each group, standard deviation, and sample size (n) is provided. The group of individuals which have failed to reproduce is denoted 0, and group of reproduced individuals 1. Successful and unsuccessful rearing experience of mother examines the effect of having a mother that either reared her offspring to a dispersal age successfully (number of offspring that survived >1 year of being born) or unsuccessfully (number of offspring that survived <1 year of being born).

L’Hoest’s monkey (Females)						
Risk factor	Mean ($\pm$ St.dev)		n		Test statistic	P-value
	0	1	0	1		
Age at first transfer (months)	82.8 $\pm$ 39.4	57.8 $\pm$ 22.4	12	16	$t_{20}=2.33$	0.03
Number of transfers	1.1 $\pm$ 0.5	0.9 $\pm$ 0.7	13	24	$W=182.5$	0.34
Potential partners	1.7 $\pm$ 2.7	2.4 $\pm$ 1.2	13	23	$W=70$	0.008
Group min	3.15 $\pm$ 2.4	4.3 $\pm$ 2.2	13	23	$W=100$	0.1
Group max	5.7 $\pm$ 2.7	9.0 $\pm$ 3.0	13	23	$W=67.5$	0.007
Age of dam (years)	10.6 $\pm$ 2.6	8.5 $\pm$ 2.7	11	19	$t_{22}=2$	0.06
Reproductive experience of mother	9.5 $\pm$ 3.7	6.6 $\pm$ 3.5	13	24	$W=229$	0.02
Successful rearing experience of mother	7.1 $\pm$ 2.7	4.7 $\pm$ 2.2	13	24	$W=233.5$	0.01
Unsuccessful rearing experience of mother	2.4 $\pm$ 1.8	1.9 $\pm$ 1.5	13	24	$W=181.5$	0.42
Experienced sibling	1 $\pm$ 0	0.92 $\pm$ 0.28	13	24	$\chi^2=0.10$	0.76
Allo-parenting	0.8 $\pm$ 0.4	0.7 $\pm$ 0.5	13	24	$\chi^2 < 0.001$	0.99
Experienced other females giving birth	0.6 $\pm$ 0.5	0.8 $\pm$ 0.4	13	24	$\chi^2 = 1.153$	0.29

Table 4: The results of statistical analysis of the association between reproductive success and social factor for captive male L'Hoest's monkeys. Mean value for each group, standard deviation, and sample size (n) is provided. The group of individuals which have failed to reproduce is denoted 0, and group of reproduced individuals 1. Successful and unsuccessful rearing experience of mother examines the effect of having a mother that either reared her offspring to a dispersal age successfully (number of offspring that survived >1 year of being born) or unsuccessfully (number of offspring that survived <1 year of being born).

L'Hoest's monkey (Males)						
Risk factor	Mean ($\pm$ St.dev)		n		Test statistic	P-value
	0	1	0	1		
Age at first transfer (months)	58.4 $\pm$ 23.7	79.9 $\pm$ 47.5	19	14	$t_{18} = -1.6$	0.14
Number of transfers	0.96 $\pm$ 0.6	1.7 $\pm$ 1.3	19	14	W=136.5	0.04
Potential partners	0.7 $\pm$ 0.6	3.2 $\pm$ 2.5	23	18	W=44	<0.001
Group min	4.35 $\pm$ 2.37	3.2 $\pm$ 1.86	23	18	W=267	0.11
Group max	7.9 $\pm$ 2.8	8.3 $\pm$ 2.8	23	18	$t_{39} = -1.49$	0.15
Age of dam (years)	7.9 $\pm$ 2.8	10.4 $\pm$ 4.8	23	10	$t_{12} = -1.5$	0.17
Reproductive experience of mother	9.5 $\pm$ 2.3	6.1 $\pm$ 4.1	23	18	$t_{26} = 3.2$	0.003
Successful rearing experience of mother	7.0 $\pm$ 2.0	4.6 $\pm$ 2.7	23	18	W=324	0.002
Unsuccessful rearing experience of mother	2.5 $\pm$ 1.5	1.5 $\pm$ 1.8	23	18	W=274.5	0.07
Experienced sibling	1 $\pm$ 0.2	0.9 $\pm$ 0.3	23	18	$\chi^2 = 0.05$	0.83
Allo-parenting	0.7 $\pm$ 0.5	0.6 $\pm$ 0.5	23	18	$\chi^2 = 0.81$	0.37
Experienced other females giving birth	0.7 $\pm$ 0.5	0.7 $\pm$ 0.5	23	18	$\chi^2 < 0.001$	1

Table 5: The results of statistical analysis of the association between reproductive success and social factors for captive male Roloway monkeys. Mean value for each group, standard deviation, and sample size (n) is provided. The group of individuals which have failed to reproduce is denoted 0, and group of reproduced individuals 1. Successful and unsuccessful rearing experience of mother examines the effect of having a mother that either reared her offspring to a dispersal age successfully (number of offspring that survived >1 year of being born) or unsuccessfully (number of offspring that survived <1 year of being born).

Risk factor	Roloway monkey (Males)				Test statistic	P-value
	Mean ($\pm$ St.dev)		n			
	0	1	0	1		
Age at first transfer (months)	56 $\pm$ 11.8	60.8 $\pm$ 11.2	10	10	t ₁₈ = -0.21	0.84
Number of transfers	1.2 $\pm$ 1.0	1.9 $\pm$ 1.2	14	13	W=63	0.16
Potential partners	2.3 $\pm$ 1.4	3.9 $\pm$ 1.8	14	13	t ₂₂ =-2.5	0.02
Group min	1.9 $\pm$ 0.6	2 $\pm$ 0.6	10	13	W=59.5	0.7
Group max	4.1 $\pm$ 2.6	6.9 $\pm$ 2.1	10	13	W=26.5	0.02
Age of dam (years)	12 $\pm$ 4.3	10.4 $\pm$ 2.9	12	7	W=50	0.52
Reproductive experience of mother	7.5 $\pm$ 3.3	8.1 $\pm$ 3.2	13	7	W=22.5	0.26
Successful rearing experience of mother	6.4 $\pm$ 3.1	7.3 $\pm$ 3.0	13	7	W=36	0.47
Unsuccessful rearing experience of mother	1.1 $\pm$ 0.1	0.9 $\pm$ 0.9	13	7	W=49.5	0.77
Experienced sibling	0.8 $\pm$ 0.4	0.9 $\pm$ 0.4	12	7	χ^2 <0.001	1
Allo-parenting	0.6 $\pm$ 0.5	0.7 $\pm$ 0.5	12	7	χ^2 =0.006	0.94
Experienced other females giving birth	0.5 $\pm$ 0.5	0.7 $\pm$ 0.5	13	7	χ^2 =0.38	0.54

Table 6: The results of statistical analysis of the association between reproductive success and social factors for captive female Hamlyn's monkeys. Mean value for each group, standard deviation, and sample size (n) is provided. The group of individuals which have failed to reproduce is denoted 0, and group of reproduced individuals 1. Successful and unsuccessful rearing experience of mother examines the effect of having a mother that either reared her offspring to a dispersal age successfully (number of offspring that survived >1 year of being born) or unsuccessfully (number of offspring that survived <1 year of being born).

Risk factor	Hamlyn's monkey (Females)				Test statistic	P-value
	Mean ($\pm$ St.dev)		n			
	0	1	0	1		
Age at first transfer (months)	135.1 $\pm$ 56	106.1 $\pm$ 89.5	8	12	W=59	0.42
Number of transfers	1.3 $\pm$ 1.1	1.5 $\pm$ 1.2	14	13	W=61	0.67
Potential partners	1.9 $\pm$ 0.8	3.1 $\pm$ 0.5	9	15	t ₁₄ = -1.1	0.29
Group min	1.9 $\pm$ 1	2.8 $\pm$ 1.5	8	12	W=27	0.1
Group max	2.8 $\pm$ 1.4	5.3 $\pm$ 1.8	8	12	W=13	0.007
Age of dam (years)	9 $\pm$ 2.5	8.8 $\pm$ 3.4	9	15	t ₂₁ =0.17	0.87
Reproductive experience of mother	2.8 $\pm$ 1.1	4.7 $\pm$ 1.5	9	15	t ₂₁ = -3.70	0.001
Successful rearing experience of mother	2.6 $\pm$ 1.1	4.4 $\pm$ 1.6	9	15	t ₁₇ = -3.14	0.006
Unsuccessful rearing experience of mother	0.2 $\pm$ 0.4	0.3 $\pm$ 1.1	9	15	W=72.5	0.68
Experienced sibling	0.8 $\pm$ 0.4	1 $\pm$ 0	9	15	χ^2 =3.64	0.14
Allo-parenting	0.6 $\pm$ 0.5	0.7 $\pm$ 0.5	9	13	χ^2 =0.43	0.67
Experienced other females giving birth	0.6 $\pm$ 0.5	0.5 $\pm$ 0.5	13	7	χ^2 =0.01	1

Table 7: The results of statistical analysis of the association between reproductive success and social factors for captive female Diana monkeys. Mean value for each group, standard deviation, and sample size (n) is provided. The group of individuals which have failed to reproduce is denoted 0, and group of reproduced individuals 1. Successful and unsuccessful rearing experience of mother examines the effect of having a mother that either reared her offspring to a dispersal age successfully (number of offspring that survived >1 year of being born) or unsuccessfully (number of offspring that survived <1 year of being born).

Diana monkey (Females)						
Risk factor	Mean ($\pm$ St.dev)		n		Test statistic	P-value
	0	1	0	1		
Age at first transfer (months)	96.9 $\pm$ 38.2	61.6 $\pm$ 40.2	12	16	t ₂₄ =2.37	0.026
Number of transfers	0.68 $\pm$ 0.58	0.81 $\pm$ 1	19	32	W=306	0.97
Potential partners	1.6 $\pm$ 1.5	4.2 $\pm$ 4	19	34	W=159.5	0.004
Group min	2.4 $\pm$ 1.8	3.7 $\pm$ 2.5	17	31	W=166	0.03
Group max	5.1 $\pm$ 1.7	9.7 $\pm$ 7.6	17	31	W=153	0.02
Age of dam (years)	11.3 $\pm$ 0.5	11 $\pm$ 0.6	19	19	t ₃₆ =0.53	0.6
Reproductive experience of mother	4.9 $\pm$ 2.6	4.2 $\pm$ 2.9	19	30	W=344.6	0.22
Successful rearing experience of mother	4.3 $\pm$ 2.5	3.9 $\pm$ 2.8	19	30	W=232	0.43
Unsuccessful rearing experience of mother	0.6 $\pm$ 1	0.3 $\pm$ 0.7	19	30	W=325.5	0.28
Experienced sibling	0.7 $\pm$ 0.5	0.5 $\pm$ 0.5	19	30	χ^2 =0.95	0.33
Allo-parenting	0.5 $\pm$ 0.5	0.3 $\pm$ 0.5	19	30	χ^2 =0.86	0.36
Experienced other females giving birth	0.5 $\pm$ 0.5	0.8 $\pm$ 0.4	19	30	χ^2 =6.18	0.013

Table 8: The results of statistical analysis of the association between reproductive success and social factors for captive male Diana monkeys. Mean value for each group, standard deviation, and sample size (n) is provided. The group of individuals which have failed to reproduce is denoted 0, and group of reproduced individuals 1. Successful and unsuccessful rearing experience of mother examines the effect of having a mother that either reared her offspring to a dispersal age successfully (number of offspring that survived >1 year of being born) or unsuccessfully (number of offspring that survived <1 year of being born).

Risk factor	Diana monkey (Males)				Test statistic	P-value
	Mean ($\pm$ St.dev)		n			
	0	1	0	1		
Age at first transfer (months)	65.6 $\pm$ 20.6	55 $\pm$ 23.9	12	22	t ₂₆ =1.35	0.19
Number of transfers	0.87 $\pm$ 0.5	1.88 $\pm$ 1.19	15	24	W=93.5	0.006
Potential partners	3.2 $\pm$ 2.8	4.1 $\pm$ 2.8	15	24	W=144	0.3
Group min	3.9 $\pm$ 4.4	3.0 $\pm$ 3.1	13	24	W=163	0.66
Group max	5.2 $\pm$ 6.0	8 $\pm$ 5.8	13	24	W=60.5	0.003
Age of dam (years)	9.1 $\pm$ 3.6	10.2 $\pm$ 3.5	14	9	t ₁₈ = -0.72	0.48
Reproductive experience of mother	6.3 $\pm$ 3.3	3.3 $\pm$ 2.5	15	19	W=222	0.002
Successful rearing experience of mother	6.1 $\pm$ 3.2	3.1 $\pm$ 2.1	15	19	W=227	0.003
Unsuccessful rearing experience of mother	0.2 $\pm$ 0.4	0.2 $\pm$ 0.5	15	19	W=154.5	0.52
Experienced sibling	0.6 $\pm$ 0.5	0.5 $\pm$ 0.5	14	19	χ^2 =0.37	0.54
Allo-parenting	0.5 $\pm$ 0.5	0.2 $\pm$ 0.4	14	19	χ^2 =1.88	0.17
Experienced other females giving birth	0.5 $\pm$ 0.5	0.7 $\pm$ 0.5	15	24	χ^2 =0.19	0.66

Table 9: The risk assessment of the effect of the investigated social factors on sub-optimal reproduction in European zoo L’Hoest’s monkeys. High risk assessment category indicates an important effect on reproductive success, whereas low category indicates little impact on the reproductive success. Significant results found for females (F) and males (M), are indicated. The numbers refer to articles in the reference section of this paper.

L’Hoest’s monkey				
Risk factor	Supported by studbook data	Supported by peer-reviewed articles	Risk assessment	Uncertainty
Age at transfer	Yes (F)	63	High	Medium
Number of transfers	Yes (M)	20	High	Medium
Number of potential partners	Yes (F & M)	24, 25, 39, 40, 44, 55	High	Low
Group size	Yes (F)	38, 51, 58	High	Medium
Age of dam	No	-	Low	Medium
Previous reproductive experience and successful rearing experience	Yes (F & M)	16	High	High
Allocare	No	6, 7, 15, 18, 35, 53	Low	High
Sibling experience	No	30, 64	Low	Medium
Experience of other female giving birth	No	-	Low	Medium

Table 10: The risk assessment of the effect of the investigated social factors on sub-optimal reproduction in European zoo Hamlyn's monkeys. High risk assessment category indicates an important effect on reproductive success, whereas low category indicates little impact on the reproductive success. Significant results found for females (F) and males (M), are indicated. The numbers refer to articles in the reference section of this paper.

Hamlyn's monkey				
Risk factor	Supported by studbook data	Supported by peer-reviewed articles	Risk assessment	Uncertainty
Age at transfer	No	63	Low	Medium
Number of transfers	No	20	Low	Medium
Number of potential partners	No	24, 25, 39, 40, 44, 55	Low	High
Group size	Yes (F)	38, 51, 58	High	Medium
Age of dam	No	-	Low	Medium
Previous reproductive experience and successful rearing experience	Yes (F)	16	High	Medium
Allocare	No	6, 7, 15, 18, 35, 53	Low	High
Sibling experience	No	30, 64	Low	Medium
Experience of other female giving birth	No	-	Low	Medium

Table 11: The risk assessment of the effect of the investigated social factors on sub-optimal reproduction in European zoo Roloway monkeys. High risk assessment category indicates an important effect on reproductive success, whereas low category indicates little impact on the reproductive success. Significant results found for females (F) and males (M), are indicated. The numbers refer to articles in the reference section of this paper.

Roloway monkey				
Risk factor	Supported by studbook data	Supported by peer-reviewed articles	Risk assessment	Uncertainty
Age at transfer	No	63	Low	Medium
Number of transfers	No	20	Low	Medium
Number of potential partners	Yes (M)	24, 25, 39, 40, 44, 55	High	Low
Group size	Yes (M)	38, 51, 58	High	Medium
Age of dam	No	-	Low	Medium
Previous reproductive experience and successful rearing experience	No	16	Low	High
Allocare	No	6, 7, 15, 18, 35, 53	Low	High
Sibling experience	No	30, 64	Low	Medium
Experience of other female giving birth	No	-	Low	Medium

Table 12: The risk assessment of the effect of the investigated social factors on sub-optimal reproduction in European zoo Diana monkeys. High risk assessment category indicates an important effect on reproductive success, whereas low category indicates little impact on the reproductive success. Significant results found for females (F) and males (M), are indicated. The numbers refer to articles in the reference section of this paper.

Diana monkey				
Risk factor	Supported by studbook data	Supported by peer-reviewed articles	Risk assessment	Uncertainty
Age at transfer	Yes (F)	63	High	Medium
Number of transfers	Yes (M)	20	High	Medium
Number of potential partners	Yes (F)	24, 25, 39, 40, 44, 55	High	Low
Group size	Yes (F & M)	38, 51, 58	High	Medium
Age of dam	No	-	Low	Medium
Previous reproductive experience and successful rearing experience	Yes (M)	16	High	High
Allocare	No	6, 7, 15, 18, 35, 53	Low	High
Sibling experience	No	30, 64	Low	Medium
Experience of other female giving birth	Yes (F)	-	High	Medium

Table 13. The summary of social risk factors showing high or medium risk to the overall reproductive success in zoo guenons. Potential mitigating actions are proposed along with further research areas. Summary shows which guenon species and what sex was significantly affected (F=Female, M=Male).

Step in risk pathway	Risk factor	Guenon species and sex	Potential mitigating actions/research required
Compatibility and Behavioural Experience Health and Behaviour Maternal and Paternal Behaviour	Age at first inter-facility transfer	L'Hoest's (F) Diana (F)	Time inter-facility transfer earlier in female maturity (optimally 3 years of age in Diana monkey, 5 years of age in L'Hoest's monkey) Further research needed to understand this trend
Health and Behaviour	Number of inter-facility transfers	L'Hoest's (M) Diana (M)	Ensure males are moved at least once from their natal group and consider subsequent transfers as a beneficial social management practice Research into mimicking wild dispersal patterns through inter-facility transfers
Compatibility and Behavioural Experience Fertility	Number of breeding partners	L'Hoest's (F, M) Diana (F) Roloway (M)	Allow higher number of genetically adequate breeding partners Research into implementing mate choice using behavioural indicators of mate competency
Compatibility and Behavioural Experience Health and Behaviour Maternal and Paternal Behaviour	Group size	L'Hoest's (F) Hamlyn's (F) Diana (F, M) Roloway (F, M)	Consider expanding group size for each species Research required to confirm our findings due to limitations associated with the nature of our data
Compatibility and Behavioural Experience Fertility Health and Behaviour Maternal and Paternal Behaviour	Previous reproductive experience and successful rearing experience	L'Hoest's monkey (F, M) Hamlyn's monkey (F) Diana monkey (M)	Research needed to understand the negative impact of greater reproductive and rearing experience of the mother on the reproductive success of offspring

Figures

Figure 1: The risk pathway illustrating where each social factor fits along the pathway to reproductive success.

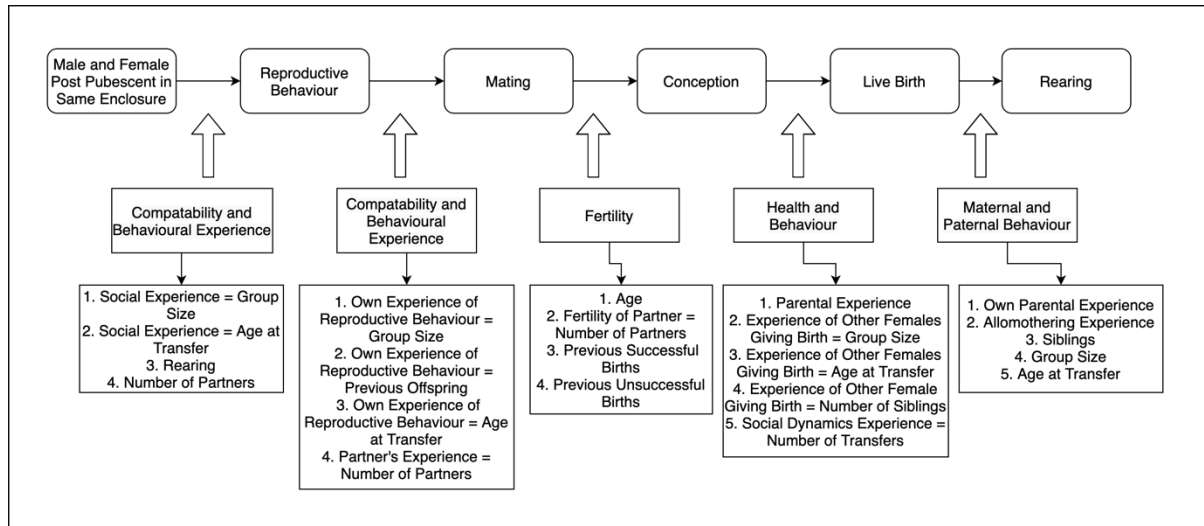


Figure 2: Statistically significant associations found in the analysis of reproductive success and social factors in female L’Hoest’s monkeys: A. the age at first inter-facility transfer, B. the number of potential partners, C. maximum group size, D. reproductive experience of the mother (the number of offspring the mother has had), E. successful rearing experience of the mother (the number of offspring the mother has reared to at least one year of age). Plots show mean value for each group and error bars indicate standard deviation.

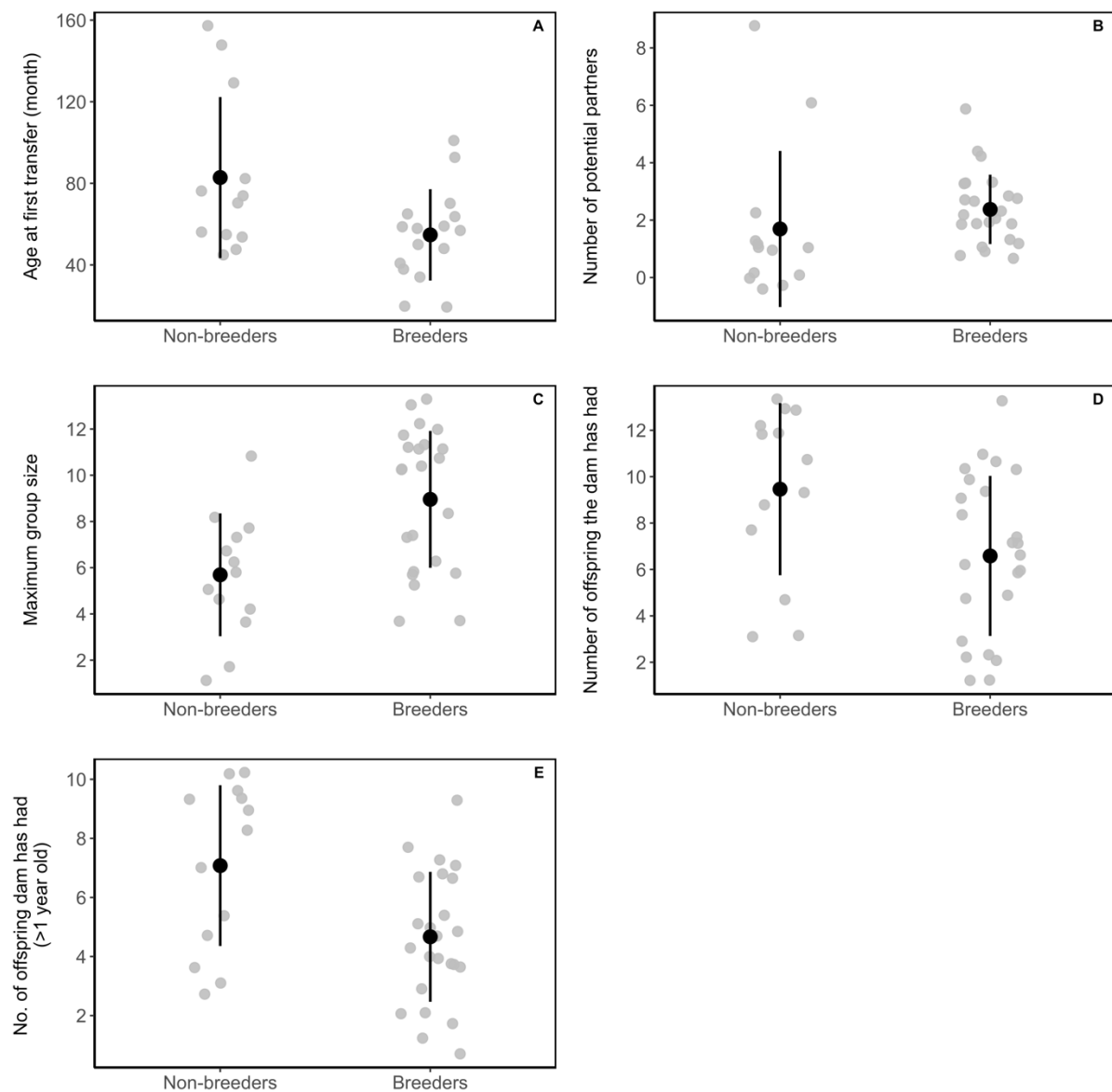


Figure 3: The statistically significant associations found in the analysis of reproductive success and social factors in male L’Hoest’s monkeys: A. the number of transfers, B. the number of potential partners, C. reproductive experience of the mother (the number of offspring the mother has had), D. successful rearing experience (the number of offspring the mother has reared to at least one year of age). Plots show mean value for each group and error bars indicate standard deviation.

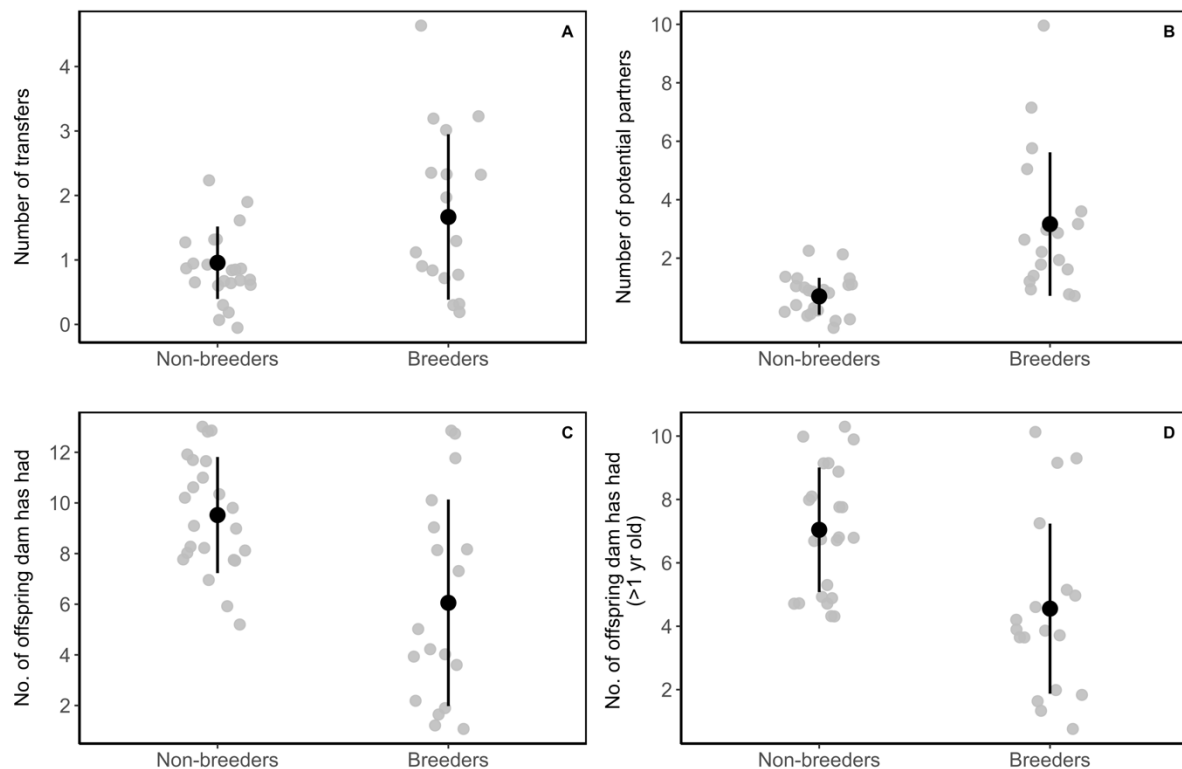


Figure 4: Statistically significant associations found in the analysis of reproductive success and social factors in male Roloway monkeys: A. the number of potential partners, B. maximum group size. Plots show mean value for each group and error bars indicate standard deviation.

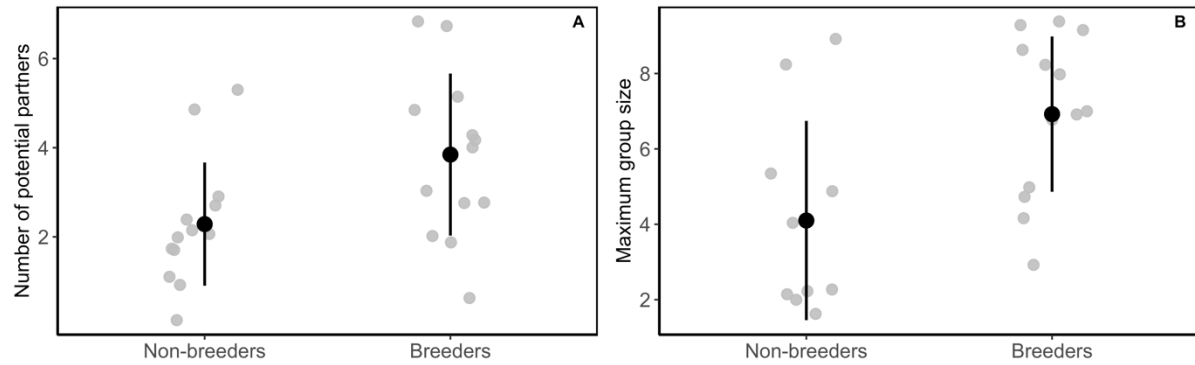


Figure 5: Statistically significant associations found in the analysis of reproductive success and social factors in female Hamlyn's monkeys: A. maximum group size, B. reproductive experience of the mother (the number of offspring the mother has had) C. successful rearing experience (the number of offspring the mother has reared to at least one year of age). Plots show mean value for each group and error bars indicate standard deviation.

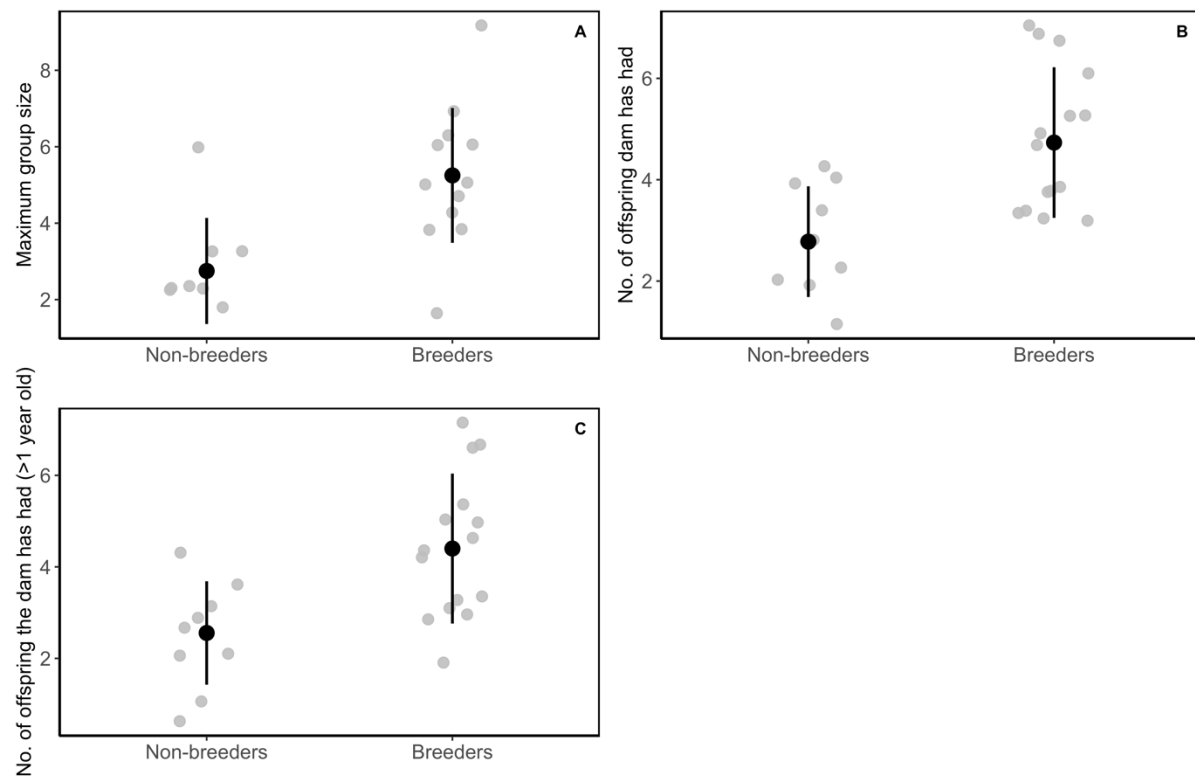


Figure 6: Statistically significant associations found in the analysis of reproductive success and social factors in female Diana monkeys: A. the age at first inter-facility transfer, B. the number of potential partners, C. minimum group size, D. maximum group size, E. the experience of other female giving birth. Plots show mean value for each group and error bars indicate standard deviation.

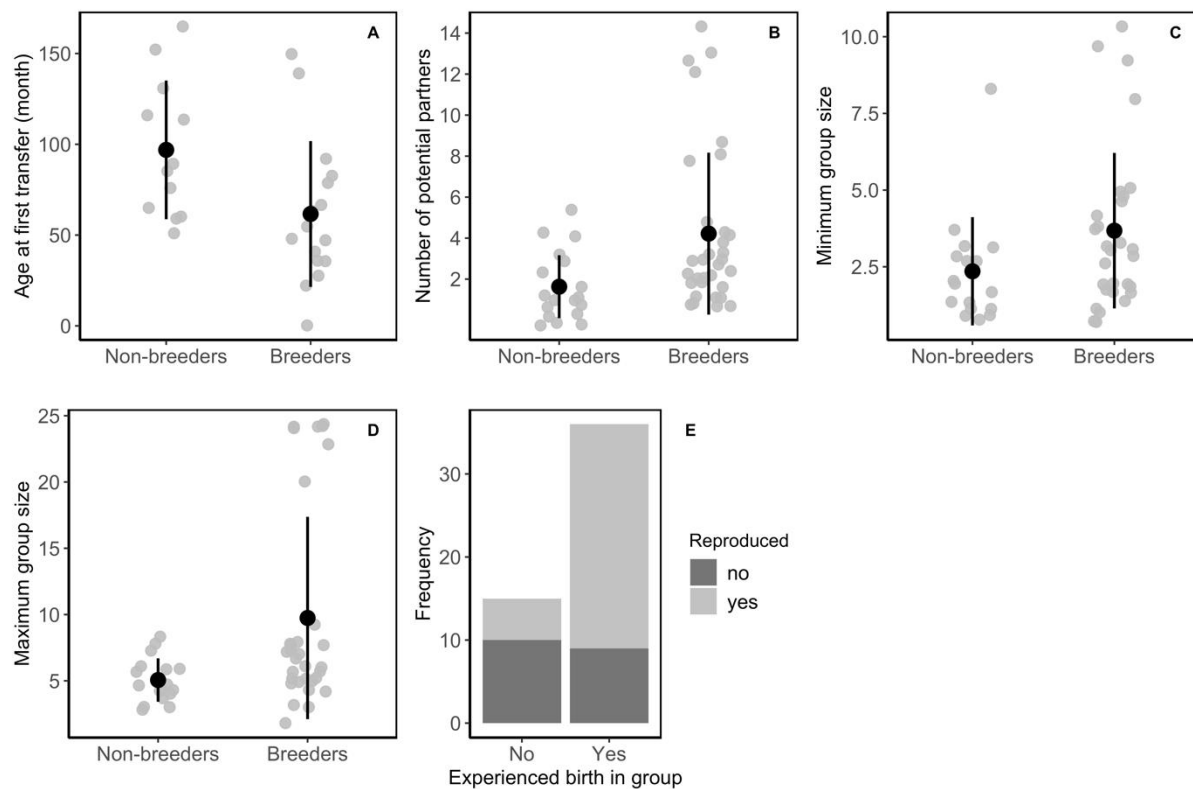


Figure 7: Statistically significant associations found in the analysis of reproductive success and social factors in male Diana monkeys: A. number of inter-facility transfers, B. maximum group size, C. reproductive experience of the mother (the number of offspring the mother has had), D. successful rearing experience (the number of offspring the mother has reared to at least one year of age). Plots show mean value for each group and error bars indicate standard deviation.

