Controlling inbreeding rate in the European zoo population of Hamadryas baboons Papio hamadryas with a breeding circle

2 authors, including:

Jeroen Kappelhof
Royal Rotterdam Zoological & Botanical Gardens

3 PUBLICATIONS   **7** CITATIONS

Controlling inbreeding rate in the European zoo population of Hamadryas baboons *Papio hamadryas* with a breeding circle

Jeroen Kappelhof[1,2] and Jack J. Windig[1]

[1]*Animal Breeding and Genomics, Wageningen University & Research, PO Box 338, 6700 AH Wageningen, The Netherlands*
[2]*Royal Rotterdam Zoological & Botanical Gardens, PO box 532, 3000 AM Rotterdam, The Netherlands*

Correspondence: Jack J. Windig, email; jack.windig@wur.nl

Abstract
Genetic management based on kinships can be difficult to apply for animals living in groups without reliable pedigrees and with limited control over mating. Rotational mating is an alternative for which no pedigrees are needed. This study used computer simulations to estimate the effect of a breeding circle for the European zoo population of Hamadryas baboons *Papio hamadryas*. The breeding circle consisted of the 14 zoos with the largest populations in Europe. New-born females were transferred using a fixed scheme from Zoo 1 to Zoo 2, Zoo 2 to 3, 3 to 4 etc. and from Zoo 14 to Zoo 1. Frequency and number of transferred females varied. Breeding circles reduced inbreeding levels compared to a situation without exchange between zoos, while genetic diversity levels were almost the same. Without exchange between zoos, inbreeding rate per generation of the whole population was 1.93%. With a breeding circle, it ranged between 0.64% and 1.47%. Increased frequency of transfers and number of transferred females resulted in lower inbreeding rates. Within zoos, high inbreeding rates (up to 12.3%) without exchange disappeared with breeding circles (up to 2.3%). With random exchange between zoos, inbreeding rates were higher than with a breeding circle. Genetic diversity after 100 years was almost the same (98.5%) for no exchange, random exchange and with breeding circles. Breeding circles can thus be, at least sometimes, an effective way to genetically manage zoo populations in a way that is not labour intensive.

Introduction

In the 1980s, European zoos began breeding programmes in order to develop stable, self-sustaining captive populations to ensure their survival for future generations (Rivas Moreno et al. 2018). In addition, the European Association of Zoos and Aquaria (EAZA) was established in 1992 to oversee and facilitate these breeding programmes. Since its establishment, EAZA's top priority has been sustaining genetically healthy zoo populations (Rivas Moreno et al. 2018), and one of its tasks is to oversee and facilitate breeding programmess. Currently, there are over 400 EAZA Ex-situ Programmes (EEPs) and European Studbooks (ESBs) managed by EAZA zoos. In parallel, the IUCN has set up guidelines for ex-situ management in species conservation

(McGowan et al. 2017), outlining a five-step approach into which genetic management should be integrated. Genetic management is needed for all programmes and studbooks to maintain genetic diversity, as much as possible, into the long term. Therefore, inbreeding rates should be minimised and its reciprocal, effective population size, maximised, as these determine the loss of genetic diversity (Falconer and Mackay 1996, Frankham et al. 2002). In most captive populations, this means that studbook keepers aim to maintain the inbreeding rate per generation to below 1%, the advised maximum for a genetically healthy population (FAO 1998). Recently, together with the Conservation Planning Specialist Group (CPSG) and other regional zoo and aquarium associations, EAZA launched a new process called the Integrated Collection Assessment and Planning (ICAP) workshop (Traylor-Holzer et al. 2019). The aim

of such workshops is to provide a comprehensive assessment of every breeding programme that will enhance species conservation by providing guidance to zoos and aquariums on conservation priorities. Moreover, these workshops need to bring synergy between in-situ and ex-situ efforts to conserve a species, also called the One Plan Approach (OPA) (Traylor-Holzer et al. 2019).

Currently, management of zoo populations is generally based on mean kinship of individuals, defined as the average of the kinship an individual has with all individuals (including itself) in the population (Ballou et al. 2004). Pairings between relatively unrelated animals that each have a low mean kinship is preferred, because they have relatively few relatives in the population and are more likely to carry rare alleles. By using this method, both inbreeding and loss of genetic diversity can be minimised. However, although this method proved its success in many breeding programmes, it also has limitations (Ballou and Lacy 1995). These limitations apply, for example, to animals that live in social groups with a complex hierarchy, or animals that live in (large) groups where it is difficult to identify individuals. For these species it is difficult or sometimes even impossible to construct correct individual pedigrees or to have control over mating pairs (Wang 2004). Managing a population based on mean kinship of individuals needs a correct pedigree or DNA information, because otherwise mean kinship of individuals cannot be calculated. For groups, one may estimate expected mean kinship within and between groups and use these to decide how many animals to exchange between which groups (Wang 2004); but this requires knowledge on historic group sizes and past exchanges between groups. Moreover, for mean kinship based management, reproductive control is also needed to determine the number of offspring per individual (Mucha and Komen 2015).

Both limitations apply to the European captive population of Hamadryas baboons *Papio hamadryas.* This population contains 1,162 individuals, housed in different groups divided over 34 EAZA zoos. At this moment only 9.1% of animals registered in the pedigree have known parents (Emile Prins, personal communication). Moreover, existing pedigree information can be unreliable, as was shown in two Dutch zoos (Emmen Zoo and Dierenpark Amersfoort) with DNA verification (unpublished results). In addition, the complex multi-levelled social system of Hamadryas baboons with harem leaders siring most offspring prevents the arrangement of favourable matings based on mean kinship (Kummer 1968; Colmenares 1992; Colmenares et al. 2006; Swedell et al. 2011).

Because of the inappropriateness of the current common method of genetic management for zoo populations of animals living in social groups, the genetic management of these kinds of populations is still undeveloped or even completely absent in zoos (Leus et al. 2011; Jiménez-Mena et al. 2016). This also accounts for the EAZA population of Hamadryas baboons, for which an EEP was just established in 2019 (EAZA TAG reports 2019). Moreover, populations of species with a dominant male hierarchy, such as Hamadryas baboons, may have much larger inbreeding rates compared to populations where individuals pass on their genes more equally to the next generation (Mucha and Komen 2015).

A tool that may provide a solution for this problem is rotational mating. Several forms of rotational mating exist, but the general idea is that the whole population is divided in multiple groups and that males are transferred from one group to another in such a way that females are never mated with males born in their own group (Nomura and Yonezawa 1996). This idea of rotational mating tries to combine the best of both worlds of the Single Large Or Several Small debate (SLOSS debate). This debate states that, on the one hand, genetic diversity can be preserved by dividing a population in different sub-populations, each preserving its own distinct genetic diversity. On the other hand, dividing a population

into small sub-populations without exchange between them increases inbreeding rates within these sub-populations (Margan et al. 1998).

One of the forms of rotational mating is a breeding circle in which males are exchanged in a circular way. In this form, Group 1 provides males for Group 2, Group 2 provides males for Group 3 and so on until the last group which provides males for Group 1 (Windig and Kaal 2008). This kind of genetic management can be applied to zoo populations of social animals as well. It can cope with incorrect pedigrees and can even operate without pedigree data at all (Nomura and Yonezawa 1996). Besides this, making use of a breeding circle also has practical advantages for zoos, as breeding circles can be constructed in such a way that travel distances for the different donor-recipient combinations are minimal (Windig and Kaal 2008; Mucha and Komen 2015).

Rotational mating already has proved to be successful in increasing the effective population size and reducing inbreeding levels of small populations of livestock (Windig and Kaal 2008; Mohktari et al. 2015; Windig et al. 2019). However, literature on this subject remains scarce. In addition to this, zoo populations could be genetically managed properly using rotational mating (Mucha and Komen 2015), but at this moment there are no tests using data from real zoo populations. Another gap in knowledge is how many animals, and at what frequency, need to be exchanged in order for breeding circles to be effective. Up to now, in all investigations, all animals of a single sex of each generation were rotated upon birth. One may expect that the effect diminishes if fewer animals are exchanged or animals are exchanged less frequently. This study investigates the effect of rotational mating in Hamadryas baboons in European zoos, because it is a species with incomplete pedigree records, a social structure preventing full control over mating patterns and frequencies, and because molecular data had shown that introduction of females from Cologne Zoo to Emmen Zoo resulted in lower relatedness and inbreeding levels (unpublished results). For these reasons, a breeding circle may be a suitable tool for the genetic management of the European zoo population of Hamadryas baboons, and this study investigates whether this is the case. In particular this study addressed the following questions:

1. What is the benefit of using a breeding circle in comparison to no exchange between zoos?
2. What is the effect of the number of animals exchanged between zoos?
3. What is the effect of the frequency of exchanging animals between zoos?

Materials and methods

European baboon population
Population data were obtained from the programme Zoological Information Management System (ZIMS) in September 2017. The population contained 1,162 individuals divided over 34 zoos (Table 1). Data from four zoos (Bandholm, Neunkirch, Aalborg and Kiskutlig) were discarded because of a lack of information on the sex of the animals present. Data from three other zoos (Hamburg, Katowice and Le Pal) were discarded because their populations contained only males and therefore breeding in these zoos is not possible, for the moment. Individuals without a registered sex were not considered breeding animals and were omitted from the analysis. Thirteen zoos with 10 females or fewer were also not considered in the breeding circle, because not enough females were present to be exchanged in some of the simulated breeding circles. Data of the 14 remaining zoos were used in the simulation of the breeding circles (Table 1).

All females in the population were considered a breeding female, so it was assumed that every female was a member of a harem

Table 1. Number of Hamadryas baboons present in EAZA member zoos in Europe in September 2017, and number of breeding animals simulated to investigate effects of a breeding circle.

Zoo	Country	Number of animals in zoos			Used in simulation		
		Males	Females	Unknown sex	Breeding males	Breeding females	N
Madrid	Spain	58	92		23	92	115
Emmen	Netherlands	55	67	2	14	67	81
Hilvarenbeek	Netherlands	11	41	9	8	41	49
Augsburg	Germany	29	38		10	38	48
Amersfoort	Netherlands	21	36	1	11	36	47
Koln	Germany	38	29		8	29	37
Paignton	UK	27	26	1	7	26	33
Berlin Zoo	Germany	14	20	3	5	20	25
Hodenhagen	Germany	13	20	1	5	20	25
Malton	UK	5	19	6	5	19	24
Nyiregyha	Hungary	3	19	16	3	19	22
Munich	Germany	11	15		4	15	19
Warsaw	Poland	11	12		3	12	15
So Lakes	UK	1	12	8	1	12	13
Bandholm	Denmark			91			
Neunkirch	Germany			79			
Aalborg	Denmark	1	1	33			
Pontscorf	France	12	2	5			
Lisbon	Potugal	10	8				
Farjestadt	Sweden	7	7	3			
Pecs	Hungary	5	10				
Frankfurt	Germany	5	7				
Liberec	Czech Republic	2	9				
Copenhagen	Denmark	2	9				
Kiskutlig	Hungary			11			
Skanakv	Sweden	2	7				
La Plaine	France	2	5				
Hamburg	Germany	4	0	3			
Budapest	Hungary	2	5				
Le Pal	France	8	0				
Krefeld	Germany	2	3				
Pelissane	France	1	3				
Katowice	Poland	4	0				
Bratislava	Slovakia	1	1				
Total		364	523	272	107	446	553
Mean		11	16	8	8	32	40

and had the opportunity to breed. This is in line with observations in zoos and in the wild, because there is no evidence of solitary females (Kummer 1968). Data from Wildlands, Dierenpark Amersfoort and Hilvarenbeek showed that the average number of females per harem in their groups was around four (Job Stumpel; Raymond van der Meer; Lars Versteege, personal communication). Number of breeding males was thus derived by dividing the number of breeding females in a group by four and rounding up.

When this number was lower than the number of males present in the zoo, it was assumed that the remaining males did not have a harem and did not participate in breeding; for example, because they were too young or too old. This estimation of four lies within the range of one to eight females per harem that is seen in the wild (Swedell et al. 2011). In situations where the derived number of breeding males in a group was higher than the actual number of breeding males, the latter was used. For the three zoos (Emmen

Zoo, Dierenpark Amersfoort and Hilvarenbeek) from which the exact number of harems and so the exact number of breeding males was known, those specific numbers were used.

Simulation tool

The applicability of a breeding circle for the European Hamadryas baboon zoo population was tested with stochastic computer simulations using GenManSim (https://genebankdata.cgn.wur.nl/software/software.html). GenManSim was originally created for simulating genetic management of dog breeds (Windig and Oldenbroek 2015; Windig and Doekes 2018). The effect of different kinds of genetic management, including the use of rotation schemes, on the inbreeding level and inbreeding rate per generation can be evaluated.

The programme uses individual-based stochastic population modelling. It creates a dataset representing the population in the computer, with the sex, age or age class, sub-population, and relatedness with all other animals for each animal. To do so, it uses input that can be easily generated from studbook data. For example, rather than simulating birth rates and mortality rates the user provides the number of breeding animals and the percentage of animals in each age class for each sex. The latter can be readily derived from data in a studbook using the ages of fathers and mothers at the time of birth of their offspring. On the one hand, it is easier for users to determine actual numbers per age class instead of finding out birth and mortality rates, while on the other hand it is often not clear in a captive population to what extent numbers are caused by biological processes or by a decision of the population manager to cull more or fewer animals. Since the purpose of the software is to determine the influence of genetic management, there is no need to try to disentangle the underlying causes of the population numbers.

The number of breeding females and the number of litters are the input parameters determining the percentage of females giving birth each year. Females can produce only one litter per year. For each litter, a female is chosen at random from the breeding females. Generally, the number of litters per year will be smaller than the number of breeding females so that not all females will give birth to a litter each year. In real life, females not producing in a year can be due to a variety of reasons such as stillbirth, contraception, not being mated, or all offspring being culled or sterilised. Since these causes are generally difficult to determine, the number of litters born per year, which can be readily determined in the studbook, is used as input. There is, however, the possibility to restrict the use of certain females, for example, based on their mean kinship, so that not all females are available for breeding. In these cases, there may be not enough females available for all litters so that fewer litters are born that year. Lower fertility of females at a later age is accounted for by having a lower percentage of breeding females in the later age classes.

For each litter, a male is selected at random from the available breeding males as a father. Males may sire more than one litter in a year. Because of their random choice, the number of litters per sire will approach a Poisson distribution. However, restrictions may apply, such as a maximum relatedness allowed between the father and the mother. Moreover, there is the possibility to indicate popular sires, or dominant males. These males are selected first as the father until they have reached their designated contribution, after which the remaining males are chosen at random for the remaining litters.

To determine litter size, the user gives the percentage of litters per size (1, 2, 3, n young per litter) as input, which can also be determined readily from studbook data. The programme then draws a litter size according to these percentages. Consequently, variation in offspring per animal is due to being selected as a parent or not, variation in litter size itself and variation in lifespan as a breeding animal.

When animals age a year, the number of breeding animals in each age class is adjusted by culling animals or recruiting animals from the juvenile classes so that the original age structure is restored. In this way, a population is simulated whereby numbers stay constant. The assumption is that population managers keep the population constant, for example, for economic reasons or in order to not overpopulate a farm or a zoo. When there are fewer animals than in the previous age class, the excess is culled. When there are more animals than in the previous age class this would induce a shortage. Therefore, juvenile animals that are not reproducing are simulated as for age classes that have a lower number of breeding animals than the next age class. The number of breeding animals plus juveniles is then equal to the next age class so that upon aging, enough animals are available in the next age class. Except for these juveniles, only breeding animals are simulated. Culled animals are chosen at random, unless restrictions apply, such as the maximum number of offspring a male is allowed to sire. In real life, animals may remain in the population after their reproductive life, for example, after sterilisation, in old age or any other cause preventing animals from further reproduction, but in the programme they are removed from the simulation.

Culled animals are replaced by animals born in the previous year. When not enough animals were born in that year, the population will decrease in size and populations or sub-populations may go extinct. Populations can also go extinct if (too) many restrictions apply for mating or if restrictions are too strict. An example is when only animals are allowed to reproduce that have an inbreeding level below a certain level and as a consequence not enough animals are born.

The population can be split into sub-populations. The user provides the number of breeding animals per sex and per sub-population and whether animals can be exchanged between sub-populations. Exchange can be restricted to a single sex and according to age. The user provides either the probability that an animal migrates from one sub-population to another, or the number of animals that migrate each year. Males may also inseminate females in another sub-population, without leaving their sub-population. In that case, the user provides the probability that a litter is sired by a father of their own or another sub-population, or the number of litters sired by fathers from each (other) sub-population. Sub-populations may go extinct when too many animals migrate to other sub-populations without being replaced by new-born animals or animals migrating into that sub-population.

Simulation of European Hamadryas baboon population

A breeding circle was simulated using data of the European Hamadryas zoo population. Data on population structure, life history and breeding policies used in the simulation are either extracted from the studbook (ZIMS database) or from information of the breed managers in Emmen Zoo (Job Stumpel, personal communication) and Dierenpark Amersfoort (Raymond van der Meer, personal communication). It was assumed that females would produce one offspring at most every 5 years, following the contraception policy practiced in Emmen Zoo (Job Stumpel, personal communication), thus simulations were run for breeding cycles of 5 years. It was also assumed that on average 50% of females produced one viable offspring per 5 years, as juvenile mortality in Emmen Zoo and Dierenpark Amersfoort was 47% (data extracted from the ZIMS database). Sub populations from the 14 zoos were simulated with 12 females or more so that, on average, six or more females were born every 5 years and were available per zoo for exchange with other zoos (Table 1). Breeding circles were simulated by exchanging juvenile females (i.e. females

Table 2. Age distribution of the parents used in simulations. Age classes are each representing 5 years.

Age (years)	Class	Percentage offspring Sires	Percentage offspring Dams
1-5	1	7	24
6-10	2	50	44
11-15	3	32	20
16-20	4	11	7
21-25	5	0	5

born in the past 5 years that had not yet reproduced) between zoos. Because of the complex multi-levelled social system of Hamadryas baboons characterised by male dominance that can cause tensions within a group, sometimes resulting in severe fights, zoos are reluctant to exchange males (Emile Prins, Job Stumpel and Raymond van der Meer, personal communication). On the other hand, experience introducing females in Emmen Zoo showed that they were readily accepted in the population (Job Stumpel, personal communication). Therefore, only females were exchanged between zoos in the simulations. In the simulations, females that were transported to the next group were chosen at random from the available juvenile females in the donor zoo.

Sex ratio and age structure were based on the situation in Emmen Zoo and Dierenpark Amersfoort for which detailed data were available. All simulations were simulated for 20 breeding cycles, corresponding to 100 years. Mean age of first pregnancy for females was 3 years and 11 months (3–6 years) in a captive population of Hamadryas baboons in Australia (Birrell et al. 1996). In the simulations, females reproduced in the first breeding

Figure 1. Average inbreeding coefficient of newborn pups per 5-year breeding cycle. Solid line: one fully random mating population; dotted line, 14 zoo populations without exchange of animals; dashed line, breeding circle with five animals per zoo per 5-year breeding cycle exchanged.

cycle, thus with a mean age of 5 years, slightly higher than in the Australian population. Further age structure (Table 2) was based on studbook data collected by Emmen Zoo and Dierenpark Amersfoort.

At the start of all simulations, animals were considered unrelated to each other and non-inbred, because long-term effects are considered small (Rudnick and Lacy 2008). Population data from ZIMS shows that 50 offspring were born in 2016; as 5-year breeding cycles were simulated, this corresponds to a number of births per breeding cycle of 250. All births involved one single young; no twins or larger litters were born as reported for both wild and captive Hamadryas populations (Kummer 1968; Abbeglen 1984; Colmenares 1992; Colmenares et al. 2006).

Breeding circle evaluation
Initially, inbreeding and genetic diversity was evaluated for a breeding circle where each zoo exchanged five animals in each 5-year period. Genetic diversity was defined as 1 – f, where f is the average kinship in the population (Frankham et al. 2002). Exchange was as follows: five juvenile females were transported from Group 1 to Group 2, five animals from Group 2 to Group 3 and so on, until Group 1 received five animals from Group 14. The order of zoos in the breeding circle was based on size (Table 1). Thus, Madrid was assigned Group 1 in the breeding circle, Emmen Zoo Group 2 and So Lakes the last group. As a control, three simulations were run with no exchange, one single population and random exchange, respectively.

To evaluate the effect of the number of animals exchanged and the frequency of exchange, 12 different set-ups of breeding circles were simulated. Four different frequencies combined with three different numbers of animals transported per rotation were simulated. The simulated frequencies of rotation were: once every 5, 10, 15 or 20 years. The simulated numbers of animals transported from group to group per rotation were: one, five or 10 animals per rotation. Larger numbers could not be exchanged because insufficient animals are born in the smaller zoo populations.

All simulations were repeated 25 times to account for stochastic variation. Research by Windig and Kaal (2008) found that mean inbreeding rate per generation hardly changes when simulations are repeated more than 20 times. Inbreeding levels and remaining genetic diversity after 100 years were used to evaluate the different scenarios, as well as inbreeding rates (ΔF) within zoos and for the whole population. Inbreeding rate (or its inverse realised effective population size) evaluates the loss of genetic diversity under random mating and is directly related to the increase of homozygosity in a population and the expression of recessive genetic defects (Falconer and Mackay 1996). Inbreeding rates per zoo without exchange were compared with theoretically expected inbreeding rates estimated from the number of breeding animals assuming random mating and non-overlapping generations using $\Delta F = 1/4Nf + 1/4Nm$ with Nf (Nm) being the number of breeding females (males) (Falconer 1981).

Random exchange
Effects of a breeding circle where exchange is organised in a systematic way was compared to random exchange between zoos. In this simulation, each breeding female to be replaced because of old age, by a juvenile female, had a 90% chance of being replaced by a juvenile female born in her own zoo, and a 10% chance of being replaced by a juvenile female from another zoo. In the latter case, the female was randomly chosen from all juvenile females in all other zoos and thus the selection depended on the number of females born in all zoos. Since there was a 10% chance of being exchanged, and 250 newborns were produced per breeding cycle, of which 125 on average were female, an average of 12.5 young
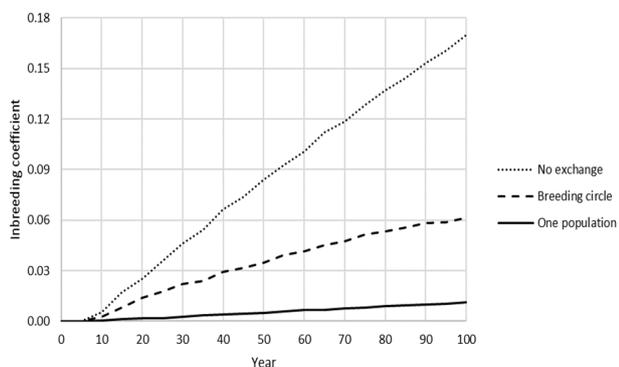
were exchanged per breeding cycle, which is slightly less than the 14 animals exchanged per breeding cycle in the scheme with one animal exchanged per 5 years.

Results

Effect of the breeding circle
Without a breeding circle and without exchange between zoos, inbreeding levels after 100 years were on average 0.170 (Figure 1). If all animals were placed in a single population with random mating, inbreeding levels were considerably lower, reaching only 0.011 on average. With a breeding circle exchanging five animals per 5 years, inbreeding levels lay in between, at 0.061 after 100 years. The genetic diversity in Year 100 was almost the same for the breeding circle and no exchange between zoos (98.47% and 98.48%, respectively), and on average slightly higher than for one large population (98.6%). In case of no exchange between zoos, inbreeding levels after 100 years within zoos varied considerably, depending on the size of the zoos, ranging from 0.058 for the largest zoo population (Madrid) to 0.603 for the smallest (So Lakes). Inbreeding levels within zoos under a breeding circle were smaller, except for the largest zoo (Madrid) and more similar to each other compared to no exchange, ranging from 0.059 to 0.163.

The inbreeding rate per generation for the whole European population without exchange between zoos amounted to 1.93%. Within zoos, the inbreeding rate varied from 0.68% in the largest group (Madrid) to 12.65% in the smallest group (So Lakes). Inbreeding rates within zoos estimated via the simulation programme were similar to inbreeding rates estimated from the number of breeding animals (Table 3). When animals were exchanged between zoos in a breeding circle, inbreeding rates decreased in all zoos. When five animals per zoo were exchanged once every 5 years, the inbreeding rate per generation for the whole population was 0.87%. Within zoos, inbreeding rates varied from 0.59% in Madrid to 2.23% in So Lakes. The decrease in inbreeding rate was strongest for the smaller zoos and consequently rates were more similar across zoos than without exchange. Although all groups benefited from the breeding circle, the smallest zoos benefited most.

Effect of frequency of exchange
The more frequently animals were rotated, the more the mean inbreeding rate per generation decreased (Figure 2). When 10 animals were rotated every 5 years, the inbreeding rate decreased to 0.64% per generation compared to 1.14% when animals were rotated every 20 years.

Effect of number of animals exchanged
Transporting more animals per rotation led to lower mean inbreeding rates (Figure 3). Transporting one animal every 10 years per rotation resulted in an inbreeding rate of 1.16%. Inbreeding rate decreased to 1.02% when five animals were rotated and to 0.88% when 10 animals were rotated.

Of the 12 combinations of frequencies and number of animals exchanged that were simulated, breeding circles realising inbreeding rates below 1% per generation were observed in four cases (Table 5). Variation in inbreeding rate between runs was smaller than in scenarios without exchange, with ranges between 0.13% and 0.39% per scenario. Genetic diversity after 100 years was very similar in all scenarios, ranging from 98.4% to 98.5%.

Random exchange
When every newborn female had a 10% chance of being transported to another zoo (i.e. on average 12.5 animals per breeding cycle) inbreeding rate was 1.19% and ranged between repeats from 1.07% to 1.37%. This was higher than exchanging one

Table 3. Expected inbreeding rate per zoo population when no exchanges take place estimated by calculation from the number of breeding males and females, and by simulation taking overlapping generations into account and expected inbreeding rate when a breeding circle is in operation in which 5 females are transferred every 5 years per zoo, estimated with computer simulation.

Zoo	Class census size	No exchange simulation	Breeding circle simulation
Madrid	0.68%	0.68%	0.59%
Emmen	1.09%	1.11%	0.77%
Hilvarenbeek	1.85%	1.84%	1.13%
Augsburg	1.56%	1.59%	0.95%
Amersfoort	1.47%	1.52%	0.91%
Koln	2.00%	1.94%	0.91%
Paignton	2.27%	2.22%	0.97%
Berlin Zoo	3.13%	3.10%	1.06%
Hodenhagen	3.13%	3.14%	1.04%
Malton	3.13%	3.31%	1.06%
Nyiregyha	5.00%	4.46%	1.63%
Munich	3.85%	3.90%	1.78%
Warsaw	5.00%	5.00%	1.60%
So Lakes	12.50%	12.65%	2.23%
Total population		1.93%	0.87%

female per zoo per 5-year breeding cycle (=11.2% or 14 animals per 5-year breeding cycle). Within zoos, inbreeding rates were higher with random exchange for all zoos except the largest. The genetic diversity after 100 years was slightly higher for random exchange (98.5%) compared to exchanging one female per zoo per 5-year breeding cycle (98.4%).
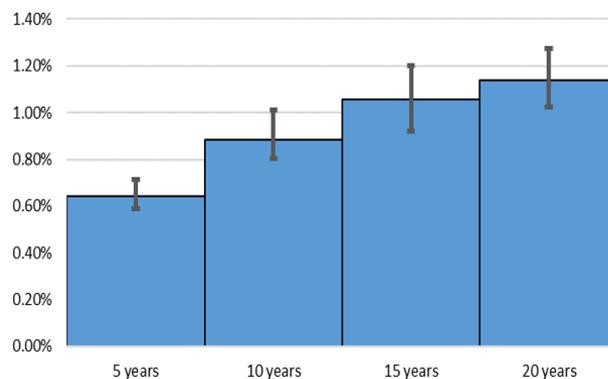

Figure 2. Mean inbreeding rate per generation in %, estimated with computer simulation for breeding circles in which 10 females are transferred per zoo with different frequencies of exchange. Bars indicate range found over 25 repeats.

Table 4. Mean inbreeding rate per generation and its range in brackets, determined with computer simulation for all rotation regimes. In brackets range observed (minimum and maximum value observed in 25 repeats).

	1 animal	5 animals	10 animals
5 year	0.84%	0.77%	0.64%
	(0.73% - 1.01%)	(0.68% - 0.87%)	(0.59% - 0.72%)
10 year	1.16%	1.02%	0.88%
	(1.01% - 1.29%)	(0.93% - 1.10%)	(0.80% - 1.01%)
15 year	1.37%	1.20%	1.06%
	(1.16% - 1.55%)	(1.08% - 1.32%)	(0.92% - 1.20%)
20 year	1.47%	1.29%	1.14%
	(1.31% - 1.60%)	(1.12% - 1.44%)	(1.03% - 1.27%)

Discussion

Genetic management of group-living species can be difficult, especially when animals cannot be recognised individually, for example, in small species of invertebrates or fish. Furthermore, even if individuals can be recognised individually, genetic management can be problematic when there can be no control over mating. Captive species form a continuum from no control over mating and without information on kinship or other population data up to full control and complete information (Smith 2010). Hamadryas baboons lie somewhere along this continuum. Individuals can be recognised, but parentage assignment can be difficult and due to the social structure there is no control over mating. When there is full control over mating and complete information on relationships, genetic management based on mean kinship is generally the most effective (Mucha and Komen
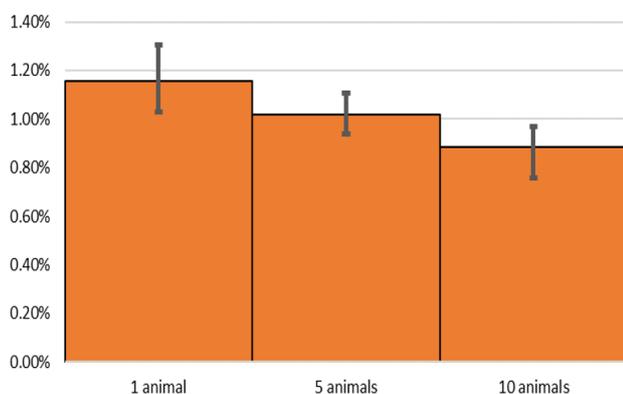

Figure 3. Mean inbreeding rate per generation in %, estimated with computer simulation for breeding circles exchanging different numbers of animals between zoos once every 10 years.

2015). Breeding circles lie at the other extreme, and can be set up without any population data other than group membership, and without any control over mating within groups.

In all simulated cases of breeding circles, inbreeding rates per generation were lower compared to no rotation at all. Importantly, the results showed that it is possible to attain inbreeding rates below 1% with a breeding circle. This is a considerable improvement to no exchange, where the inbreeding rate was below 1% in the largest zoo only. The maximum number of animals that can be exchanged is all animals of one sex each breeding cycle, and that is the standard evaluated in literature (e.g. Nomura and Yonezawa 1996). This study shows that breeding circles can be effective with only a fraction of the animals being exchanged and at a lower frequency.

Exchanging animals between zoos, or sub-populations in general, will lead to lower inbreeding rates and higher genetic diversity within zoos/sub-populations. With breeding circles, this is organised in a systematic way so that one avoids large increases in some of the zoos or for some periods, or large relatedness between animals from some of the zoos and not between others. Indeed, in the simulations, random exchange of animals resulted in higher inbreeding rates. Other rotational schemes, such as 'maximum avoidance of inbreeding' have been suggested, where the donor recipient combinations change each year or breeding cycle (Leus et al. 2011). Nomura and Yonezawa (1996) show that these schemes have similar degrees of effectiveness as was confirmed for a practical example in a Dutch sheep breed (Windig and Kaal 2008). The advantage of breeding circles over other schemes is that donor–recipient sub-populations remain the same over time, which simplifies the organisation of a breeding circle.

Results showed that rotating more frequently and more animals per rotation always resulted in a lower inbreeding rate per generation. In particular, the small groups benefited from the breeding circle having the biggest decreases in inbreeding rates. Different configurations of donor–recipient combinations are possible. A breeding circle was simulated with a reversed order of zoos, exchanging five animals each 5-year breeding cycle but inbreeding rate was almost the same (0.79% ranging from 0.72–0.85%) as in the original order. The most notable change was that inbreeding rate was lower in the largest zoo (Madrid) as well as in the smallest zoos. This can be explained by both these zoos receiving females from larger zoos in a reversed order compared to the original order. Inbreeding rates in all other zoos were higher in a reversed order. In the long-run, inbreeding rates are expected to converge between the different groups. For a breeding circle involving a sheep breed with eight different sub-populations in the form of large flocks (Windig et al. 2019), inbreeding rates per flock converged to the same level for all breeds after about 30 generations, both in computer simulations and with mathematical calculations. Further investigations are needed to determine whether it will take, for a breeding circle with 14 zoos with Hamadryas baboons, 30 generations (around 240 years) for inbreeding rates to converge.

There are still important questions to investigate, such as the optimal number of groups and group size for a breeding circle given the number of animals. This study simulated the existing situation only for the Hamadryas baboons, using the 14 largest zoos. Interestingly, overall inbreeding rate decreased somewhat, when the smallest zoo was omitted. This was due to lower inbreeding rates in the largest zoo that received females from a slightly larger zoo, when the smallest zoo was eliminated. When more zoos were removed from the simulation, inbreeding rates increased. For example, with the seven smallest zoos removed, inbreeding rate for exchanging five animals each 5 years increased to 0.91 (ranging from 0.81 to 1.08) and genetic diversity after 100 years decreased from 98.4% to 97.9%.

In the simulations, it was assumed that all animals within and between groups were unrelated to each other at the start of each simulation. Obviously, this is generally not the case in reality. In general, relatedness is higher within sub-populations and lower across sub-populations without migration (Wright 1931). For Hamadryas baboons, kinship determined with the help of DNA showed that mean kinship within Emmen Zoo was much higher between resident animals than the kinship with some females imported from Cologne Zoo (unpublished results). There have been only a couple of transports of animals between different European zoos in the past (Emile Prins, personal communication) so it is likely that kinship within zoos will be high, and between zoos generally low. The consequence of high kinship within groups and low kinship between groups was simulated for a breeding circle with sheep (Windig et al. 2019). In that case, inbreeding immediately decreased when the breeding circle was started in all flocks due to the import of relatively unrelated animals within each flock. Thereafter, inbreeding increased slowly taking about 75 years to reach the levels observed at the start of the breeding circle. For Hamadryas baboons, it is thus likely that a breeding circle will have a more positive effect than simulated here because the exchange between zoos will initially result in a decrease in relatedness, while in the simulations all animals, regardless of zoo, were not related, and consequently their inbreeding could not decrease because of exchange of animals.

The breeding circle simulated here, consisted of only 14 of the 34 zoos. These 14 zoos contain approximately half of the total individuals and thus a significant part of the population remains genetically unmanaged, when such a breeding circle would be operated. In most cases, zoos were discarded from the simulation because they had fewer than 10 females in their group and therefore could not participate in the breeding circle that involved exchanging 10 individuals. Possible solutions are exchanging fewer individuals, or (virtually) grouping zoos with small numbers to allow them to exchange animals, or enlarging the small groups to participate in the breeding circle. Virtual grouping means that several smaller zoos, for example those in Hungary, together donate 10 females to a larger zoo, and together receive 10 females from a single other large zoo. Some other zoos were discarded from the simulations because they could not provide information about the sex of their Hamadryas baboons. However, assuming that when animals should be transferred, they need to be captured and then sexing of the animals should be possible, these zoos could be easily incorporated in a breeding circle, when one were to be put in practice.

Breeding circles need a constant rotation of animals at a certain frequency, contrary to genetic management by mean kinship where transfers between zoos takes place occasionally. On the other hand, when operating a breeding circle, distances between the donating and receiving zoo can be minimised, since the order of a breeding circle is probably less important. Practical considerations, such as costs, both financially, organisationally and in terms of decreased welfare of animals due to transport, can therefore be taken into account when determining the order of the breeding circle.

Although breeding circles can be a useful tool for the genetic management of species that live in big groups, the kind of breeding circle needs to be tailored for every species separately, in order to attain a ΔF below 1%. In other words, because of the huge variety in social systems, age structure, size and sex ratios across species that live in groups, every species will need its own frequency of rotation and number of animals to be transported. For instance, species with bigger groups will need less rotation than species with small groups (Nomura and Yonezawa 1996). Moreover, species with groups in which the distribution of the number of offspring per sire is more equal, will need less rotation

than groups where the distribution of offspring is highly skewed. Therefore, a successful breeding circle for one species cannot be simply extrapolated to another species. Furthermore, there is the risk that animals are not chosen randomly; that is, animals with undesired behaviour or health may be sent to other zoos, or animals that are phenotypically ideal may be selected from other zoos, or only the animals that are the easiest to catch may be exchanged, or highly related animals may be grouped. In this respect, molecular tools may help to select animals based on their (average) relatedness. Nevertheless, trust will always be needed between the participating zoos so that each zoo can maintain a healthy population. Moreover, the results shown in this article are simulation-based and undoubtedly it remains a challenge to capture all the variation and stochasticity of life into any simulation. However, in the case of the Hamadryas baboon, it is argued that the assumptions made are justified, because many population management tools for this species (i.e. contraception, euthanasia) are available to population managers and therefore there is a significant level of influence by humans.

Breeding circles are not the only option for genetic management of zoo populations of (social) group-living animals. Options include management based on DNA information as proposed by Fienieg and Galbusera (2013), group pedigree analysis (Jiménez-Mena et al. 2016) or mixtures between individual kinship-based genetic management and exchanges between groups. Smith (2010) investigated combinations of mean kinship-based management and random exchange between groups. In general, genetic management was more effective with higher percentages of mean kinship-managed individuals. This paper showed that systematic exchange via a breeding circle is more effective than random exchange. It may be that a mixture of mean kinship-based management and breeding circles are more effective than breeding circles on their own, but detailed analyses are needed to confirm this. Nevertheless, when information becomes available on relatedness, either through detailed and reliable pedigrees or by genotyping, the first option to explore is to use this information for genetic management. Breeding circles are a good alternative for when such information is not available.

Hamadryas baboons are not high on the conservation priority list of zoos and nature conservationists. Taking into account costs and efforts needed to genotype all individuals, or a significant part of the captive population, genotyping is not a realistic option for the near future. In Hamadryas baboons, there have only been a few exchanges of animals between zoos, and breeding success of introduced animals is not always recorded well. Consequently, information on group relatedness based on pedigrees in Hamadryas baboons is limited. Moreover, genetic management based on group relatedness is most successful when generations are discrete and when not much breeding has already taken place (Jiménez-Mena et al. 2016), both of which do not hold for this population.

This study showed that a breeding circle can be an appropriate form of genetic management for the European Hamadryas baboon zoo population. There are multiple possible designs of a breeding circle to get ΔF below the advised maximum of 1%. Zoos are advised to investigate the possibility of setting up a breeding circle; for the largest zoos, this should be done as quickly as possible. In addition, it is advised to consider the least-intensive rotation regime needed to get ΔF below 1%, in this case once every 10 years transporting 10 animals from group to group. This would result in ΔF being 0.88%, which is below the advised maximum of 1%. The two zoos with larger groups without known sex can be easily incorporated in the breeding circle, provided that they have enough females to be transferred. Including them in the breeding circle will result in even lower inbreeding rates. Moreover, it is advised to virtually or physically fuse the small groups, that were omitted from the

current simulation, into bigger groups that can participate in the breeding circle. If this is not deemed possible, surplus animals of the breeding circle could be transported to zoos with small groups to ensure at least some genetic flow in these groups. Furthermore, it is advised for more research and consultation within the zoo community on this topic, because literature is scarce and zoos are not familiar with using breeding circles.

Acknowledgements

References

Abbeglen J. (1984) *On socialization in hamadryas baboons*. Lewisburg, PA: Bucknell University Press.

Ballou J.D., Lacy R.C. (1995) Identifying genetically important individuals for management of genetic variation in pedigreed populations. In: Ballou J.D. Gilpin M.E. Foose T.J. *Population management for survival and recovery*. Columbia University Press, New York: 76–111.

Ballou J., Briscoe D., Frankham R. (2004) *A primer of conservation genetics*. Cambridge University Press.

Birrell A.M., Hennessy A., Gillin A., Horvath J., Tiller D. (1996) Reproductive and neonatal outcomes in captive bred baboons (*Papio hamadryas*). *Journal of Medical Primatology* 25: 287-293.

Colmenares F. (1992) Clans and Harems in a Colony of Hamadryas and Hybrid Baboons: Male Kinship, Familiarity and the Formation of Brother-Teams. *Behaviour* 121: 61-94.

Colmenares F., Esteban M., Zaragoza F. (2006) One-Male Units and Clans in a Colony of Hamadryas Baboons (*Papio hamadryas hamadryas*): Effect of Male Number and Clan Cohesion on Feeding Success. *American Journal of Primatology* 68: 21-37.

EAZA TAG reports 2019 (2019) *European Association of Zoos and Aquarias* 36-38 :https://www.eaza.net/assets/Uploads/Annual-report/TAG-reports-2019-webLR.pdf

Falconer D.S., Mackay T.F.C. (1996) *Introduction to quantitative genetics*, Longman Group, Harlow.

Farid A., Makarechian M., Strobeck C. (1987) Inbreeding under a cyclical mating system. *Theoretical and Applied Genetics* 73: 506–515.

Fienieg E.S., Galbusera P. (2013) The use and integration of molecular DNA information in conservation breeding programmes: a review. *Journal of Zoo and Aquarium Research* 1: 44–51.

Food and Agriculture Organization (1998) *Secondary guidelines for the management of small populations at risk.* FAO, Rome, Italy.

Frankham R., Ballou, J.D., Briscoe D.A. (2002) *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK.

Honda T., Nomura T., Mukai F. (2004) Reduction of inbreeding in commercial females by rotational mating with several sire lines. *Genetics Selection Evolution* 36: 509–526.

Jiménez-Mena B., Schad K., Hanna N., Lacy R.C. (2016) Pedigree analysis for the genetic management of group-living species. *Ecology and Evolution* 6: 3067–3078.

Kummer H. (1968) *Social organization of hamadryas baboons; a field study.* University of Chicago Press.

Leus K., Traylor-Holzer K., Lacy R.C. (2011) Genetic and demographic population management in zoos and aquariums: recent developments, future challenges and opportunities for scientific research. *International Zoo Yearbook* 45 213–225.

Margan S.H., Nurthen R.K., Montgomery M.E., Woodworth L.M., Lowe E.H., Briscoe D.A., Frankham R. (1998) Single Large or Several Small? Population Fragmentation in the Captive Management of Endangered Species. *Zoo Biology* 17: 467–480.

McGowan P.J.K., Traylor-Holzer K., Leus K. (2017) IUCN guidelines for determining when and how ex situ management should se ssed in species conservation. *Conservation Letters* 10: 361–366.

Mokhtari M.S., Miraei-Ashtiani S.R., Jafaroghli M., Gutierrez J.P. (2015) Studying Genetic Diversity in Moghani Sheep Using Pedigree Analysis. *Journal Agricultural Science and Technology* 17: 1151–1160.

Mucha S., Komen H. (2016) Rates of inbreeding and genetic adaptation for populations managed as herds in zoos with a rotational mating system or with optimized contribution of parents. *Journal of Animal Breeding and Genetics* 133: 323–333.

Nomura T., Yonezawa K. (1996) A comparison of four systems of group mating for avoiding inbreeding. *Genetics Selection Evolution* 28: 141–159.

Rivas Moreno M., Rodríguez Teijeiro J.D., Abelló M.T. (2018) Genetic and demographic analysis of European Endangered Species Programme (EEP) and Species Survival Plan (SSP) Western lowland gorilla *Gorilla gorilla gorilla* populations. *International Zoo Yearbook* 52: 194–211.

Roe K., McConney A., Mansfield C.F. (2014) The role of zoos in modern society - a comparison of zoos reported priorities and what visitors believe they should be. *Anthrozoös* 27: 529–541.

Rudnick J.A., Lacy R.C. (2008) The impact of assumptions about founder relationships on the effectiveness of captive breeding strategies. *Conservation Genetics* 9: 1439–1450.

Smith B.R. (2010) *Genetic management of groups*. PhD dissertation, University of Maryland, College Park, USA.

Swedell L., Saunders J., Schreier A., Davis B., Tesfaye T., Pines M. (2011) Female "Dispersal" in Hamadryas Baboons: Transfer Among Social Units in a Multilevel Society. *American Journal of Physical Anthropology* 145: 360–370.

Traylor-Holzer K., Leus K., Bauman K. (2019) Integrated Collection Assessment and Planning (ICAP) workshop: Helping zoos move toward the One Plan Approach. *Zoo Biology* 38: 95–105.

Wang J. (2004) Monitoring and managing genetic variation in group breeding populations without individual pedigrees. *Conservation Genetics* 5: 813-825.

Windig J.J., Doekes H.P. (2018) Limits to genetic rescue by outcross in pedigree dogs. *Journal of Animal Breeding and Genetics* 135: 238–248.

Windig J.J., Kaal L. (2008) An effective rotational mating scheme for inbreeding reduction in captive populations illustrated by the rare sheep breed Kempisch Heideschaap. *Animal* 2: 1733–1741.

Windig J.J., Oldenbroek J.K. (2015) Genetic management of Dutch golden retriever dogs with a simulation tool. *Journal of Animal Breeding and Genetics* 132: 428–440.

Windig J.J., Verweij M.J.W., Oldenbroek J.K. (2019) Reducing inbreeding rates with a breeding circle: Theory and practice in Veluws Heideschaap. *Journal of Animal Breeding and Genetics* 136: 51–62.

Wright S. (1931) Evolution in mendelian populations. *Genetics* 16: 97–159.