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Mucha, S; Komen, H

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1 **Rates of inbreeding and genetic adaptation for populations managed as**
2 **herds in zoos with a rotational mating system or with optimized**
3 **contribution of parents**

4
5 Sebastian Mucha¹²³, Hans Komen^{1§}

6
7 ¹Animal Breeding and Genomics Centre, Wageningen University

8 P.O. Box 338, 6700 AH, Wageningen, The Netherlands

9
10 ²Department of Genetics and Animal Breeding, Poznan University of Life Sciences

11 Wolynska 33, 60-637 Poznan, Poland

12
13 ³Scotland's Rural College, Animal & Veterinary Sciences

14 Easter Bush, Midlothian EH25 9RG, United Kingdom

15
16 [§]Corresponding author

17 Wageningen University

18 P.O. Box 338, 6700 AH, Wageningen, The Netherlands

19 Email: hans.komen@wur.nl

20 Phone: +31317482465

21

22 **Summary**

23

24 This study compares two genetic management scenarios for species kept in herds, such as
25 deer. The simulations were designed so that their results can be extended to a wide range of
26 zoo populations. In the first scenario the simulated populations of size 3x20, 6x40 or 20x60
27 (herds x animals in herd) were managed with a rotational mating (RM) scheme in which
28 10%, 20% or 50% of males were selected for breeding and moved between herds in a circular
29 fashion. The second scenario was based on optimal contribution theory (OC). OC requires an
30 accurate pedigree to calculate kinship; males were selected and assigned numbers of
31 offspring in order to minimize kinship in the next generation. RM was efficient in restriction
32 of inbreeding and produced results comparable with OC. However, RM can result in genetic
33 adaptation of the population to the zoo environment, in particular when 20% or less males are
34 selected for rotation and selection of animals is not random. Lowest rates of inbreeding were
35 obtained by combining OC with rotation of males as in the RM scheme. RM is easy to
36 implement in practice and does not require pedigree data. When full pedigree is available, OC
37 management is preferable.

38

39 Keywords: optimal contribution, rotational mating, breeding circle, zoo populations

40

41 **Introduction**

42

43 Maintenance of genetic diversity is particularly important for small populations of wild
44 animals maintained in zoo gardens. Currently zoos have a rich portfolio of breeding programs

45 that includes more than 500 species survival plan (SSP) programs managed by Association of
46 Zoos and Aquariums (AZA 2014), and 388 European Endangered species Programs (EEP)
47 and the European StudBook (ESB) programs managed by European Association of Zoos and
48 Aquaria (EAZA 2014). The aim of these programs is to make every effort to ensure that
49 genetic diversity of captive populations is maintained. The key in this case is to maintain
50 adequate genetic and demographic structure, which will ensure steady growth of the
51 population over many generations (Lees & Wilcken 2009). Cooperation is indispensable here
52 as many zoo populations are isolated and too small to conduct a balanced breeding program
53 (Lees & Wilcken 2009).

54 The aim of every genetic conservation program is to minimize the loss of genetic diversity,
55 and to control rates of inbreeding as much as possible. However, some reports (Earnhardt et
56 al. 2001; Zimmermann et al. 2007) suggest that a number of breeding programs in zoos
57 achieve sub-optimal results. According to Long et al. (2011) the median of gene diversity
58 retained for 264 SSP populations is 92% and it is predicted to fall to 67% in 100 years. It is
59 also worth mentioning that 38% of the AZA populations retain less than 90% of genetic
60 diversity of the founding populations (Long et al. 2011). This points to the need to optimize
61 breeding programs to better manage available resources. Past methods proposed for
62 conservation of genetic diversity included tools that affect mating strategies such as
63 maximum avoidance of inbreeding (Wright 1921), which can be efficient in the short term
64 but may result in high inbreeding in the long term (Caballero & Toro 2000), and tools to
65 maintain genetic diversity like population fragmentation and breeding in isolated herds to
66 conserve genetic diversity on the meta-population level (Leus et al. 2011). However, the
67 latter strategy is not recommended for small herds as inbreeding will rapidly increase,
68 resulting in inbreeding depression and accumulation of deleterious alleles (Whiteley et al.
69 2015). Currently, mating of animals based on mean kinship is the main method used for

70 management of zoo populations (Leus et al. 2011). Mean kinship is the mean of the kinship
71 coefficients of a given individual with every individual in the population including itself.
72 Priority is given to matings of animals with low mean kinship as they have few relatives in
73 the population and are likely to carry alleles that are rare in the population (Ballou & Lacy
74 1995). Determination of parents and their contributions to the next generation has to be
75 followed by a decision on how to mate the animals. This can be achieved through a two-step
76 approach, where first contributions are allocated to the animals and subsequently mating pairs
77 are optimised (Fernandez & Caballero 2001; Sonesson & Meuwissen 2000), or a single-step
78 approach that optimises both parameters at the same time (Ballou & Lacy 1995; Fernandez et
79 al 2001). Fernandez et al. (2001) evaluated performance of both methods using simulations
80 and concluded that the amount of genetic diversity preserved by the two methods was quite
81 similar, but the single-step method was more flexible and assured compatibility between the
82 contributions of males and females. This should therefore lead to overall higher levels of
83 genetic diversity. A more recent simulation study by Ivy & Lacy (2012) explored the above
84 mentioned mating strategies with an additional layer of complexity such as variable mortality
85 rate, reproductive rate, pairing success rate and reproductive success rate. As a result dynamic
86 mean kinship strategy (two-step approach) was recommended as optimal for populations of
87 mammals with low fecundity and long lifespans (Ivy & Lacy 2012).

88 Implementation of kinship-based management poses several difficulties that are related to the
89 limitations of zoo breeding programs. Zoo populations usually have a very limited capacity
90 that restricts the number of animals which can be kept in the population. Therefore, to
91 maintain the populations in good condition and avoid overcrowded zoo environment, it is
92 necessary to either transfer part of the animals to another zoo or to cull them. Transferring of
93 animals can also pose a significant challenge particularly if the animals that would form
94 optimal mating pairs are from two distant locations. Therefore it is important to take into

95 account fragmentation of the population and organise the transfer of animals that limits the
96 costs and effort involved. Additionally, with species such as deer or many other hoofstock
97 animals, it is important to account for skewed reproduction rates. Because of hierarchical
98 structure, few dominant males mate with groups of females and have high contributions,
99 whereas the majority of males have very low or zero contributions to the next generation.

100 The best known strategy to maintain genetic diversity is by optimizing the contributions of
101 the parents to minimize global kinship in their offspring (optimal contribution theory;
102 (Meuwissen 1997). In livestock this method is used to optimize genetic gain while
103 simultaneously restricting the rate of inbreeding. However, efficiency of this method depends
104 strongly on pedigree completeness (Oliehoek & Bijma 2009). It has been demonstrated that
105 with pedigrees containing gaps or misidentified parents the method does not perform well
106 (Oliehoek & Bijma 2009). Low quality of pedigree information in populations of livestock
107 and zoo animals is a common problem (Earnhardt et al. 2004; Oliehoek & Bijma 2009).
108 Incorrect entries in pedigrees are usually impossible to detect without the use of molecular
109 markers. In case of livestock, the level of pedigree errors reported in the literature is around
110 10% (Oliehoek & Bijma 2009), which can decrease efficiency of the optimal contribution
111 method.

112 On the other hand there are methods, such as rotational mating, which do not require accurate
113 pedigree records to control the increase of inbreeding (Nomura & Yonezawa 1996).

114 Rotational mating occurs in several forms, but the basic idea is that females are mated with
115 males coming from a different herd in a “round robin fashion”. Breeding circle, used
116 especially in sheep breeding, is one of the most common forms of rotational mating. It is
117 based on the strategy that each herd never uses its own males for breeding. Exchange of
118 males between herds is performed in a rotational way. The first herd provides males for the
119 second herd, the second herd provides males for the third, etc., and the last herd is the source

120 of males for the first herd (Windig & Kaal 2008). Possible errors or missing information in
121 the pedigrees do not affect performance of the method. Moreover, it can be used even in the
122 absence of pedigree data under the condition that it is possible to determine the herd of origin
123 for each animal.

124 Captive breeding programs usually aim to preserve the population so that it can be
125 reintroduced into the wild in the future (Frankham et al. 2010; Frankham 2015). The success
126 of such reintroduction widely depends on the level of wild fitness that has been preserved in
127 captivity. The mechanism of genetic adaptation to the captive environment is driven by
128 natural selection. Because zoo environments differ from the wild, the genetic variants that
129 confer the highest fitness in captivity differ from those that are beneficial in natural
130 environment (Frankham 2008). Genetic adaptation to captivity increases with selection
131 differential, genetic diversity, effective population size and generations in captivity
132 (Frankham 2008). Therefore it is important to avoid unintentional selection for characteristics
133 related to exterior appearance of the animal or personal preference of program coordinators.
134 This can be easily achieved in genetic management programs that are based on kinship, such
135 as optimal contribution theory, as it does not involve phenotypic selection, apart from natural
136 selection. On the other hand, some degree of unintentional phenotypic selection can occur
137 when only part of the animals are selected.

138 In this paper we use deer species maintained in zoos as an example to compare two strategies
139 to manage their genetic diversity. Deer populations in zoos are characterized by
140 fragmentation of the meta-population over several herds, skewed mating ratios ranging from
141 1 to 5 males per 10 females, and high variance in offspring among males caused by dominant
142 males in the herds. A recent analysis of studbooks of 15 deer species in European zoos
143 showed that most studbooks were incomplete, and that 10 out of 15 populations (species) had
144 low effective population size (between 10 and 20) with significant effect of inbreeding on

145 longevity and survival of offspring (Mucha, unpublished results). This points to the need for
146 more effective management programs. In theory, breeding circles could offer a simple
147 alternative to pedigree-based management for deer populations as deer are similar to sheep
148 populations in a number of ways such as low reproductive rate of females, division in herds
149 and males with highly variable number of offspring. Therefore, the aim of this paper was to
150 compare performance of genetic management by rotational mating (breeding circles) with
151 management based on pedigree and optimal contributions in simulated populations of deer.
152 The simulations were designed in such a way that implications of the results could be
153 extended to a wide range of zoo populations of animals with similar live histories and
154 demographics.

155

156 **Materials and Methods**

157

158 **Simulated populations**

159 Three populations were simulated that resembled small populations of deer maintained in
160 zoos in Europe. They were divided into herds resembling the actual number of zoos that bred
161 each population. The first was a large population (based on *Elaphurus davidianus*) consisting
162 of 1200 individuals per generation, divided over 20 herds (60 animals per herd). The second
163 population (based on *Cervus eldi thamin*) consisted of 240 animals, divided in 6 herds (40
164 animals per herd), and the third (*Axis calamianensis*) of only 60 individuals kept in three
165 herds (20 animals per herd). In each of the simulated populations half of the animals born
166 each generation were male and half were female. For simplicity it was assumed that animals
167 reproduced only once in a lifetime and died afterwards (discrete generations). Furthermore, to
168 maintain a constant population size in each generation, it was assumed that each female gave

169 birth to two offspring: two males, two females, or one male and one female. The average sex
 170 ratio of all offspring (population level) in each generation was 1:1. There was no selection in
 171 females as they all had to participate in the creation of the next generation in order to
 172 maintain a constant population size. For each population, three mating ratios were simulated,
 173 where all females were used along with only 50% (1:2 mating ratio), 20% (1:5 mating ratio)
 174 or 10% (1:10 mating ratio) of males. Using only 10, 20, or 50% of the available males
 175 implies that (unintentional) selection could take place, which could lead to genetic adaptation.
 176 We therefore simulated two scenarios: one with random selection of males, and one with
 177 selection of males on a single (not specified) trait with a heritability of 0.3 and phenotypic
 178 variance of 1. The effect of inbreeding depression on the simulated trait was not included in
 179 the simulation.

180 Simulations were performed for 20 generations, and replicated 50 times.

181 All founders had a phenotypic value of 0 and a genetic value calculated as:

$$182 \quad r_{norm} \sqrt{h^2 \sigma_p^2}$$

183 where: r_{norm} is a random number drawn from a normal distribution with a mean of 0 and
 184 variance of 1, h^2 is the heritability (0.3), and σ_p^2 is the phenotypic variance of the simulated
 185 trait. In every generation, each offspring was assigned a genetic value A as follows:

$$186 \quad A = \frac{1}{2} A_S + \frac{1}{2} A_D + MS$$

187 where A_S and A_D are genetic values of sire and dam, respectively. Mendelian sampling term
 188 (MS) was calculated as:

$$189 \quad MS = r_{norm} \sqrt{\frac{1}{2} \left(1 - \frac{1}{2} (F_s + F_D) \right) h^2 \sigma_p^2}$$

190 where F_S and F_D are inbreeding coefficients of sire and dam, respectively. Phenotypic value
191 of offspring was assigned as:

$$192 \quad P = A + r_{norm} \sqrt{(1 - h^2) \sigma_P^2}$$

193

194 **Rotational mating (RM)**

195 Breeding circles with discrete generations were used. In every generation the first herd
196 provided male offspring for mating with females from the second herd. The second herd
197 supplied males to the third herd et cetera. Female offspring remained in the same herd where
198 they had been born. Two scenarios were considered for selection of males (Table 1). In the
199 first scenario (1a), males were chosen at random (random selection) and rotated to the
200 neighbouring herd, where they were used for breeding. The number of selected males
201 depended on the mating ratio assumed (1:2, 1:5 or 1:10). Selected males were mated at
202 random with females. Non-selected males did not reproduce. In the second scenario (1b)
203 selection of males was based on their phenotype for the simulated trait (phenotypic selection).
204 Males with the highest trait values were selected and rotated to the neighbouring herds, where
205 they were mated at random with females.

206

207 **Optimal contribution (OC)**

208 The software package Gencont with the option “*minimise ΔF* ” (Meuwissen 1997;
209 Meuwissen, 2002) was used to determine the optimum contributions of animals to the next
210 generation in order to achieve the lowest possible rate of increase in mean pairwise kinship.
211 This was achieved by varying the contribution of each animal to the next generation (fraction
212 of offspring attributable to the parent) according to the equation:

213
$$\min(\bar{A}_p) = \mathbf{c}' \mathbf{A} \mathbf{c}$$

214 where \bar{A}_p is the lowest possible average relationship of parents; \mathbf{c} is a vector of contributions
215 of length n (n = the total number of animals in the population); \mathbf{A} is a relationship matrix of
216 selection candidates. The contributions of the selection candidates \mathbf{c} are optimized by the
217 Lagrangian multiplier method. The \bar{A}_p value has to increase over generations due to finite
218 population size which leads to increase of relationships over time.

219 In order to maintain constant population size, all females (N_f) were selected and received
220 equal contributions of $1/N_f \cdot 100\%$. Selection was performed only on the male side and their
221 contributions differed depending on their relatedness. The process was optimised so that for a
222 given number of males required for breeding (determined by the mating ratio) a set of males
223 was selected that would minimise kinship in the next generation, and their contributions were
224 varied to achieve the optimal result. The population was managed purely on kinship, thus
225 genetic gain was not expected.

226 With optimal contribution, three alternative management scenarios were considered (Table
227 1). In the first scenario it was assumed that mating was performed in a meta-population
228 without any subdivision into herds. Therefore selection and contribution of males based on
229 the optimal contribution theory was applied on a meta-population scale (OC_m). In the second
230 scenario, selection and mating was performed separately within each herd. There was no
231 exchange of animals between the herds (OC_i). The third scenario was similar to the optimal
232 contribution performed separately within each herd, but each generation males were
233 exchanged between herds in a rotational fashion similar to a breeding circle (OC_r).

234 Contributions of sires and dams to the next generation were calculated assuming all sires
235 from the neighbouring herd had been transferred to the herd of destination. Effectively, the
236 number of sires rotated between the herds was equal to the number of sires with nonzero

237 contributions. In every scenario, three mating ratios (1:2, 1:5 and 1:10) were simulated and
 238 selected males mated with randomly chosen females. The mating ratio determined the
 239 number of males with nonzero contributions selected by GENCONT in the optimal
 240 contribution based scenarios, i.e. a mating ratio of 1:2 in pop3 means that 15 out of 30 sires
 241 were selected to contribute to the next generation.

242

243 **Calculation of parameters**

244 The mean coefficient of inbreeding in each generation (\overline{F}_t) was calculated as:

$$245 \quad \overline{F}_t = \frac{\sum_{i=1}^{N_t} F_i}{N_t}$$

246 where: F_i is the inbreeding coefficient of the i -th individual from generation t , N_t is the
 247 number of individuals born in generation t

248 Increase of inbreeding per generation was calculated as:

$$249 \quad \Delta F_t = \frac{\overline{F}_t - \overline{F}_{t-1}}{1 - \overline{F}_{t-1}}$$

250 Where: \overline{F}_t and \overline{F}_{t-1} are the mean inbreeding coefficients of the whole population in
 251 generation t and $t-1$, respectively.

252 Mean increase of inbreeding in generations 5 to 20 was calculated as:

$$253 \quad \Delta F = 1 - \sqrt[15]{\frac{1 - F_{20}}{1 - F_5}}$$

254 To allow for good comparison between rotational mating and optimal contribution selection
255 schemes, generation 5 was used as starting point assuming that the population had reached
256 Bulmer equilibrium.

257 Across population mean kinship in each generation was calculated as:

$$258 \quad \overline{mk}_t = \frac{1}{N_t} \sum_{i=1}^{N_t} mk_i = \frac{1}{N_t^2} \sum_{i=1}^{N_t} \sum_{j=1}^{N_t} f_{ij}$$

259 where: mk_i is the mean coefficient of kinship of the i -th individual with the rest of the
260 population, f_{ij} is kinship between individuals i and j and N_t represents the total number of
261 individuals born in the whole population in a given generation. Mean kinship within
262 individual herds was calculated using the same formula, with N_t equal to the number of
263 individuals born in each herd in a given generation.

264 Phenotypic mean was calculated as an arithmetic mean of trait values observed in a given
265 generation. The mean genetic level was an arithmetic mean of breeding values for the
266 simulated trait in a given generation.

267

268 **Results**

269

270 **Rate of Inbreeding (ΔF)**

271 *Rate of inbreeding over time:* as expected, in all schemes that used rotational mating (RM and
272 OC_r), inbreeding rates were zero in generations 1 and 2, and at a fairly constant level
273 thereafter (Figure 1). Inbreeding rates in OC_i and OC_m schemes increased after generation 1,
274 and fluctuated across generations, especially in small populations (e.g. 60 animals, see Figure
275 1).

276 *Effects of population size and mating ratio:* for each scheme tested, rates of inbreeding
277 increased almost linearly with increasing mating ratio (Table 2). Inbreeding rate was highest
278 in the smallest population (3x 20 animals) where the mean ΔF ranged from 0.71% to 2.20%
279 (mating ratio 1:2) or from 3.11% to 10.99% per generation (mating ratio 1:10). As the
280 population size increased the mean ΔF decreased (Table 2), irrespective of scheme. Lowest
281 rates of inbreeding were recorded in the biggest population (20 x 60 animals), ranging from
282 0.03% to 0.72% at mating ratio 1:2 and from 0.14% to 3.09% at mating ratio 1:10.

283 *Effect of management scheme:* lowest rates of inbreeding were obtained when managing the
284 meta-population with optimal contribution (OCm). Rates of inbreeding <1% could be
285 achieved in populations with 240 and 1200 animals, for each mating ratio. In the smallest
286 population (60 animals), achieving a rate of inbreeding <1% was only possible with a mating
287 ratio of 1:2 (Table 2). In contrast, the highest rates of inbreeding were realized when
288 managing the populations with optimal contribution in isolated herds. In the smallest
289 population (3x20), rate of inbreeding ranged from 2.20% to 10.99% when managed with 1:2
290 and 1:10 mating ratio, respectively. Mean ΔF was smaller in the larger populations, but still
291 mostly above the 1% threshold (Table 2).

292 Rotational exchange of sires between the herds, managed with (OCr) or without optimal
293 contribution (RM), produced very similar results. Rates of inbreeding were always below 1%
294 per generation (Table 2), except for the smallest population, managed with mating ratios of
295 1:5 or 1:10.

296

297 **Kinship**

298 The mean kinship of generation 20, calculated across herds, was very similar for all
299 management schemes. Mean kinship increased with mating ratio and decreased with

300 population size. Lowest across mean kinship (0.01) was observed in the population with 1200
301 animals, divided over 20 herds. The highest values (0.30-0.49) were observed in the 3x20
302 population with a 1:10 mating ratio.

303 Managing isolated herds with optimal contribution, without exchange between herds (OCi),
304 resulted in individual herds becoming very distinct from each other. Therefore, the ‘across’
305 mean kinship of the whole population was lower in comparison to the other management
306 schemes, while the ‘within’ mean kinship was highest, ranging from 0.15 (20x60; mating
307 ratio 1:2) to 0.91 (3x20; mating ratio 1:10) (Table 2).

308 The mean kinship (within and across) of generation 20 was very similar for RM and OCr
309 schemes. Due to the exchange of males, herds were more connected than in the previous
310 scenario (OCi) which led to a higher mean kinship of the whole population.

311

312 **Inbreeding rate in RM schemes with and without unintentional selection**

313 Performance of rotational mating schemes was also evaluated in additional simulations where
314 we assumed unintentional directional selection for a single simulated trait. The results of this
315 analysis indicate that rotational mating schemes with or without selection produce very
316 similar mean inbreeding rates in all of the analysed populations, irrespective of mating ratio
317 (Table 3). However, selection for a moderately heritable trait leads to substantial increase in
318 genotypic values, up to 2 or more standard deviations from the founder mean, even in small
319 populations (Table 3). For the larger populations, this is in line with what can be theoretically
320 expected from phenotypic selection with selected proportions of 10% - 50%, a heritability of
321 0.3 and a phenotypic standard deviation of 1.

322

323 **Discussion**

324

325 Research on effective methods to reduce inbreeding in small zoo populations is particularly
326 important in the light of recent reports stating that many of the current conservation programs
327 do not meet the established demographic and genetic assumptions, which may threaten their
328 survival or adversely affect the health of animals (Lacy 2013; Leus et al. 2011). The main
329 problem according to Lacy (2013) is that many of the endangered populations have a limited
330 availability of candidates for selection and low pedigree completeness. Therefore methods
331 that can mitigate these problems are of particular value for zoo populations. Use of rotational
332 mating schemes has been evaluated for small breeds of cattle (Colleau & Avon 2008), and
333 sheep (Windig & Kaal 2008). Optimal contribution has also been studied as a tool to manage
334 livestock populations (Avendaño et al. 2003; Koenig & Simianer 2006; Sonesson &
335 Meuwissen 2000). However, to our knowledge the two methods have never been compared.
336 Particularly, they have not been studied with respect to their performance in populations of
337 zoo animals managed as herds.

338 Current analysis shows that breeding circles can be a good solution for small populations
339 maintained in zoos. They can efficiently reduce inbreeding rate with minimum data input. It
340 only requires information about herd of origin for each animal. This is sufficient to plan
341 which individuals will be transferred to another herd. Therefore, the quality of pedigrees does
342 not affect the performance of the breeding program (Windig & Kaal 2008). Moreover, simple
343 organization of breeding circles makes them easy to set up. It could be relatively easy to
344 determine which zoos would exchange animals and assign them to the breeding circle.
345 Assignment of zoos to the breeding circle could be done considering their geographical
346 locations so that animals are not transported over long distances. In case of populations where

347 the location and costs would prohibit the transfer of animals on a regular basis, the OC
348 method supplemented with only occasional exchange could be a more feasible option.
349 Additional research is needed to determine the sensitivity of rotational mating to such factors
350 as overlapping generations, frequency and complexity of rotation pattern.

351 Rotational mating appears to be a very robust method that can restrict inbreeding regardless
352 of selection pressure and pedigree completeness. However, caution is required when not all
353 animals are used for breeding, as is the case for populations where excess males are culled or
354 removed. Selection criteria in rotational mating schemes are not based on measures related to
355 genetic diversity harboured by each animal (mean kinship or heterozygosity). It relies entirely
356 on phenotypic selection which involves a risk of unintentional selection for “the best
357 animals”; this may lead to genetic adaptation to captivity (Frankham 2008). This risk can be
358 minimized by selection of males using criteria related to genetic diversity along with careful
359 management of migration rates.

360 In the rotational mating schemes all of the selected males are assumed to contribute equally
361 to the next generation. On the other hand, optimal contribution theory allows for optimizing
362 their contributions and assigning different number of progeny to each male depending on
363 their relatedness to the population. Therefore optimal contribution requires more control from
364 species coordinators allowing for a more precise management of the population.

365 Apart from the management scheme used (optimal contribution or rotational mating), the
366 major factor affecting inbreeding rate was population size. Our results demonstrate that
367 populations with less than 60 animals cannot be managed without losing genetic diversity at
368 an unacceptable rate. According to the analyses of programs run by AZA and EAZA more
369 than a third of the populations are comprised of less than 50 individuals (Leus et al. 2011;
370 Long et al. 2011). Therefore, in such small populations it is particularly important to

371 maximize the number of males that participate in mating. In the simulated populations, a
372 mating ratio of 1:2 essentially always resulted in inbreeding rates below 1% per generation.
373 Higher mating ratios (1:5 and 1:10), where a very limited number of males participated in
374 mating usually led to a rapid increase of inbreeding regardless of the management scheme.
375 This was particularly apparent in populations managed as isolated herds, though the problem
376 exists also in herds with rotational exchange of males. Our results suggest that in a population
377 with 240 animals spread over 6 herds, the rate of inbreeding can be restricted to <1% per
378 generation. Therefore six zoos or deer parks could be sufficient to conserve an endangered
379 population. This points towards the need to increase the size of populations that are
380 considered as valuable from a conservation stand point.

381 The best results in terms of kinship and rates of inbreeding were obtained when OC was
382 carried out within the meta-population. In the meta-population there are more parents,
383 resulting in lower average relatedness. On the other hand, when the population is divided into
384 isolated herds, a much lower number of parents is available, which translates into a
385 significant increase of inbreeding. In isolated herds genetic drift reduces genetic diversity
386 within herds (Frankham et al. 2010; Lacy 1987). When subpopulations become completely
387 inbred, the total genetic diversity is preserved due to genetic variability between the herds
388 (Lacy 1987). However, this approach poses a significant risk that some subpopulations will
389 suffer from inbreeding depression, and may not survive (Leus et al. 2011). Moreover, sub-
390 populations depart significantly from the founders (Chesser 1983). Therefore it is important
391 to manage both the exchange of animals between the herds and contributions of animals from
392 each herd to the next generation (Fernández et al. 2008).

393 Zoo populations usually have a very limited capacity that restricts the number of animals
394 which can be kept in the population. Therefore, to maintain the populations in good condition
395 and avoid overcrowded zoo environment, it is necessary to either transfer part of the animals

396 to another zoo or to cull them. In the latter case it is important to remove those animals that
397 are least valuable to the population. The number of animals that have to be culled (selection
398 intensity) depends on reproductive capacity of the species. Generally selection intensity will
399 be higher in males than in females, which is similar to the conditions simulated in the current
400 study, where mating ratio determined selection intensity. A selective culling strategy can also
401 increase fitness of the population by eliminating individuals with health and fertility issues.
402 The main goal of conservation programs is to select animals that are beneficial for genetic
403 diversity of the population due to their low average relatedness to the population. One must
404 also bear in mind that in certain cases also some unintentional selection for desired
405 phenotypic characteristics may take place. This may lead to genetic adaptation to captivity
406 which is undesirable from a conservation point of view (Frankham 2008). That is why in the
407 current study, breeding scenarios were evaluated with respect to their potential to restrict
408 inbreeding under no directional selection pressure and with unintentional selection. Our
409 results indicate that by using a rotational mating scheme, inbreeding can be restricted with
410 and without directional selection. However, any form of directional selection will increase
411 adaptation to captivity and loss of “wild” alleles. Therefore the choice of selection criteria
412 and breeding scheme is a crucial point in managing populations.

413 It is important to look at the current results in the light of assumptions made during the design
414 of the simulations. One of the restrictions was that animals could reproduce only once in their
415 lifetime and were replaced by their offspring thereafter (discrete generations). This
416 assumption could be valid also in real zoo populations as long as females that had produced
417 offspring were moved away from males. Otherwise, overlapping generations could be
418 accounted for in the optimal contribution algorithm, and the average coancestry would be
419 limited across generations (Meuwissen 1997). Another limitation of the simulated population
420 was connected with reproductive capacity of females. To keep a constant population size, it

421 was assumed that dams always give birth to two offspring. Removing this restriction will
422 improve the performance of the OC algorithm. Additionally, to keep a constant population
423 size, each generation all females had to be used for breeding and selection was possible only
424 among males. In real populations, where generations overlap, it would be also possible to
425 perform some selection on the female side. Using the appropriate breeding scheme, this could
426 have a positive effect on fitness of the population without detrimental effects on the rate of
427 inbreeding (Meuwissen 2009). Results obtained with the investigated methods could be
428 further improved by optimisation of mating schemes. In the current simulations it was
429 assumed that the selected animals were mated at random. Use of a two stage optimisation
430 methods, where the optimisation of contributions is followed by optimisation of mating pairs,
431 could have a positive effect on the inbreeding level and the amount of genetic diversity
432 conserved (Ivy & Lacy 2012). Another alternative could involve a single-step optimisation
433 process, where both the contributions and mating design would be optimised in one step
434 (Fernandez et al. 2001).

435

436 Comparison of optimal contributions carried out in a meta-population and in a population
437 divided into herds, showed that breeding within isolated zoos leads to a significant increase in
438 inbreeding within individual herds. Optimal contribution method performed better when it
439 was conducted within a meta-population. However, due to organizational issues global
440 management of geographically separated herds can be a problem. Therefore, a combination
441 of the optimal contribution method with rotational mating might be a better alternative. In
442 this situation, optimal contribution method would be carried out separately within each herd.
443 Additionally, each generation males would be exchanged between the neighbouring zoos.
444 Comparison of optimal contribution method with rotational mating demonstrated that they
445 perform equally well. Simulations showed that rotational mating can efficiently reduce the

446 inbreeding rate. Moreover inbreeding rate in breeding circles with and without selection
447 pressure was similar. Therefore unintentional selection does not reduce the efficiency of this
448 scheme with respect to restriction of inbreeding. On the other hand, optimal contributions
449 require more control over the conservation scheme by varying the contributions of animals to
450 the next generation. However, optimal contribution requires complete and accurate pedigree
451 records (Oliehoek & Bijma 2009), which are often unavailable (Mucha et al. unpublished
452 results). Combination of the two methods (OCr) would result in a robust scheme which slows
453 down the increase of inbreeding and works irrespective of the pedigree. Accompanied by
454 optimization of animal contributions within each herd, this scheme would give further benefit
455 depending on pedigree completeness and would not be sensitive to unintentional selection.

456

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458

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465

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546 **Table 1.** Selection criteria for males, their contributions to the next generation and exchange
 547 between herds.

Scenario	Selection	Contributions	Exchange	Abbreviation
Rotational	Random	Equal contributions	Between herds	RM
	Mass			
Optimal contribution	Kinship	Optimal contribution theory	Across meta-population	OC _m
			Between herds	OC _r
			Within herds, no exchange	OC _i

548

549

Table 2. Inbreeding rate (ΔF^1), and mean kinship within and across herds after 20 generations of selection.

Population Size ²	mating ratio	RM			OC _m		OC _i			OC _r		
		ΔF [%]	Kinship		ΔF [%]	Kinship	ΔF [%]	Kinship		ΔF [%]	Kinship	
			within ³	across				within ³	across		within ³	across
3x20	1:2	0.83	0.19	0.16	0.71	0.14	2.20	0.38	0.13	0.75	0.18	0.15
	1:5	1.89	0.37	0.32	1.53	0.28	4.93	0.65	0.22	1.55	0.32	0.28
	1:10	3.24	0.55	0.49	3.11	0.48	10.99	0.91	0.30	3.14	0.54	0.48
6x40	1:2	0.22	0.08	0.04	0.17	0.04	1.02	0.20	0.03	0.19	0.07	0.04
	1:5	0.52	0.15	0.09	0.37	0.08	2.30	0.39	0.07	0.40	0.12	0.08
	1:10	0.93	0.26	0.16	0.72	0.14	4.74	0.64	0.11	0.76	0.22	0.14
20x60	1:2	0.13	0.05	0.01	0.03	0.01	0.72	0.15	0.01	0.12	0.04	0.01
	1:5	0.31	0.10	0.02	0.07	0.02	1.53	0.28	0.01	0.24	0.09	0.02
	1:10	0.58	0.18	0.04	0.14	0.03	3.09	0.48	0.02	0.45	0.15	0.03

551 ¹Mean increase of inbreeding in generations 5 to 20; ²nr of herds x nr of animals in each herd; ³kinship calculated within each herd. OC_m, OC_i

552 OC_r and RM, see table 1.

Table 3. Genetic level, and inbreeding rate in breeding circles with and without random selection of males.

Scenario	mating ratio	Not random		Random	
		G^1	ΔF^2	G^1	ΔF^2
Three herds with 20 animals per herd	1:2	1.78	0.84	0.04	0.83
	1:5	2.64	1.91	0.05	1.89
	1:10	2.55	3.25	0.03	3.24
Six herds with 40 animals per herd	1:2	1.98	0.23	0.00	0.22
	1:5	3.18	0.53	0.00	0.52
	1:10	3.41	0.94	-0.01	0.93
Twenty herds with 60 animals per herd	1:2	2.01	0.14	-0.01	0.13
	1:5	3.34	0.33	-0.02	0.31
	1:10	3.79	0.61	-0.01	0.58

¹G – mean genotypic level of the population after 20 generations of selection, expressed in units of standard deviation from the mean of the founder generation.

² ΔF – inbreeding rate in %

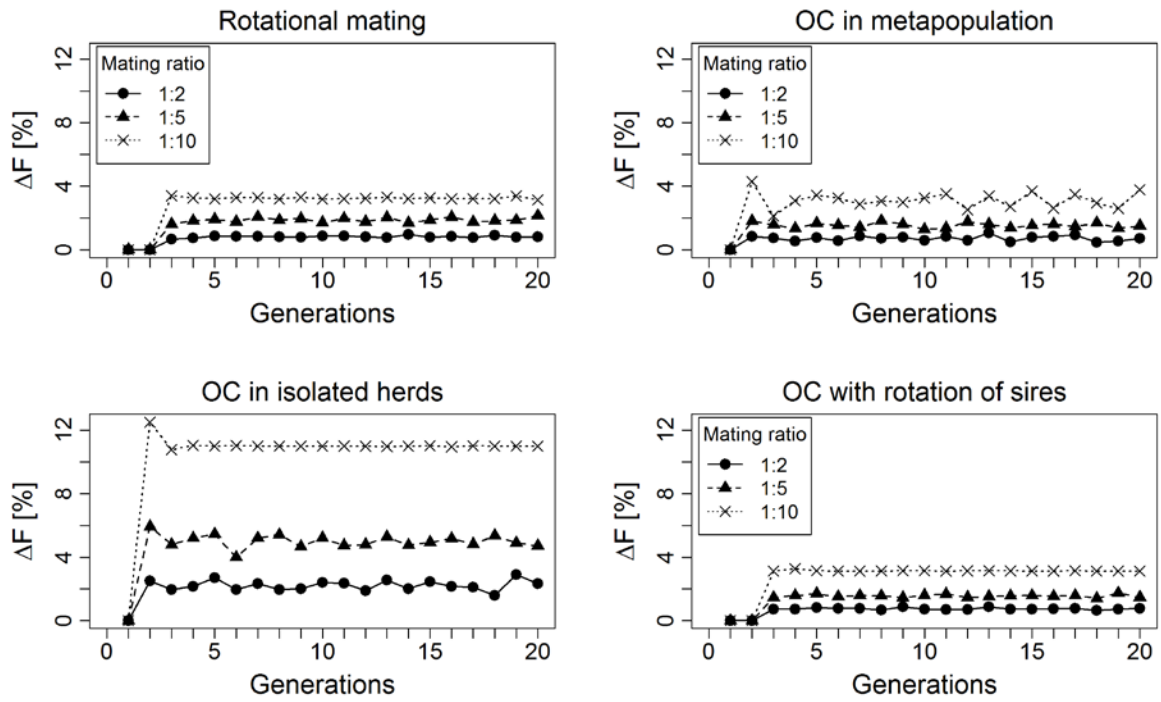


Figure1. Inbreeding rate in population of 60 animals, divided over 3 herds, managed with different scenarios