Kinship-Based Management Strategies for Captive Breeding Programs When Pedigrees Are Unknown or Uncertain

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Abstract

Zoo-based captive breeding programs typically rely on accurate pedigrees to maintain long-term population genetic diversity and prevent close inbreeding. For many mixed-sex captive populations, it is difficult to assign parentage of offspring with certainty without conducting DNA-based parentage analyses. Using the demographic parameters of a North American captive population of Arabian oryx (Oryx leucoryx), 2 kinship-based breeding-pair selection strategies were modeled for their performance in handling pedigrees with varying degrees of parentage uncertainty. We also compared these strategies with 2 nonkinship-based methods. Pedigrees simulated under different management strategies were compared for their long-term ability to maintain gene diversity (GD) and avoid inbreeding. For the Arabian oryx, results indicate that recording multiple possible parents instead of removing the unknown genomic portion of the pedigree can more efficiently utilize all animals available for breeding without compromising GD and inbreeding avoidance. Both kinship-based breeding-pair selection strategies significantly outperformed the nonkinship-based strategies.

Key words: captive breeding, genetic diversity, inbreeding, oryx, relatedness

Recent projections of population sustainability within zoos have identified an alarming number of species that cannot be demographically or genetically maintained over the long term (Lees and Wilcken 2009; Conway 2011; Lees and Wilcken 2011; Leus et al. 2011; Long et al. 2011; Lacy 2013). This is problematic not only for perpetuating exhibits but zoos frequently participate in conservation breeding programs of endangered species by maintaining populations to supply reintroduction efforts or as assurance from extinction. Zoos remain a valuable conservation resource as they maintain populations of ~15% of threatened terrestrial vertebrates (Conde et al. 2011). Unsustainability of zoo populations can, in part, be attributed to small population sizes that exacerbate genetic drift, inbreeding, and selection pressure, which can result in a potentially rapid loss of genetic diversity (Falconer 1981; Lacy 1987; Frankham et al. 2002; Frankham 2008) and reduce a species’ reproductive fitness (Ballou and Ralls 1982; reviewed in Lacy 1987, Crnokrak and Roff 1999, Keller and Waller 2002). The genetic management of captive populations is therefore an important factor in ensuring their long-term health and sustainability (Hedrick et al. 1986; Frankham 1995). Thus, the goal of genetic management is to control the rate of increase of the negative effects of inbreeding and loss of genetic diversity, including the loss of evolutionary potential.

Maximizing the genetic health and adaptability of a population requires maintaining as much of the genetic diversity that was present in the wild-born founders of a captive population as possible. Two frequently used measures of a population’s genetic diversity are gene diversity (GD), the expected heterozygosity of a population under Hardy–Weinberg equilibrium, and allelic diversity, the number of alleles at a locus. The most effective strategy to retain both GD and allelic diversity is to ensure that individuals with the lowest mean kinship (MK) reproduce (Ballou and Lacy 1995; Montgomery et al. 1997; Fernandez and Toro 1999). Kinship (f) between 2 individuals is the probability that 2 alleles randomly sampled from homologous loci, 1 from each individual, are homozygous by descent from a common ancestor (Falconer 1981). By extension, the MK of an individual is the average kinship between that individual and all other living individuals in the population including itself. Breeding pairs that are chosen based on lowest MK will also contribute to equalizing the representation of founder genomes (Ballou and Lacy 1995).

Ideally, to manage the genetics of a captive population at the individual level, a complete pedigree should be...
available. However, species that live in zoos as mixed-sex groups (herds, colonies, etc.) have been historically difficult to genetically manage, specifically in terms of selecting the most genetically valuable animals for reproduction. The parentage of offspring is often uncertain, which generates incomplete pedigrees. Additionally, within a herd setting, establishing specific breeding pairs based on minimizing kinship is generally impossible even if complete pedigrees exist. There are several nonkinship-based methods of managing genetic diversity and inbreeding in captive populations. These include subdividing populations to limit loss of allelic diversity and transferring individuals among groups periodically to avoid inbreeding (reviewed in Leus et al. 2011). However, when kinship-based management strategies are possible, they perform significantly better than these nonkinship methods (Smith 2010).

Here, we seek to examine how kinship-based breeding-pair selection performs under varying degrees of pedigree uncertainty. We test the effect of unknown and uncertain pedigrees using demographic information from captive Arabian oryx (*Oryx leucoryx*). Like the Arabian oryx, many Hippotragine antelope (i.e., addax [*Addax nasomaculatus*], scimitar horned oryx [*Oryx dammah*]) have been brought to the brink of extinction in the wild but have been successfully bred in zoos for re introduction programs. These species are often kept in relatively large herds, and the identification of sires and dams cannot be determined with absolute certainty, making kinship-based genetic management a challenge.

There are 2 commonly used options for handling uncertain pedigrees of group living captive-born individuals (i.e., not wild-born founders) so that pairwise kinship coefficients can still be calculated. The methods for calculating kinships for animals with a completely known pedigree can be extended so that the probability of parentage can be distributed over a number of possible parents (Ballou and Lacy 1995; Lacy 2012). Individual MKs are weighted by the expected contribution of all possible sires and dams to the offspring. Alternatively, the unknown or uncertain portion of an individual’s pedigree can simply be removed from kinship analyses (Willis 1993; Ballou and Lacy 1995). In this case, kinship coefficients are calculated from only the portion of each individual’s genome that can be traced back to known founders. MK is then weighted over the proportion of genomes that are known. PMx (Lacy et al. 2012; and its predecessor PM2000; Pollak et al. 2002) is a software program for the genetic and demographic management of pedigreed populations that is relied on for institutional, regional, and international captive breeding programs. PMx can calculate kinship coefficients using either method of handling uncertainty; however, the functionality and performance of these options remain untested.

Simulation is a valuable tool for assessing and validating different captive population management strategies (Sanchez et al. 2003; Fernandez et al. 2008; Ivy et al. 2009; Ivy and Lacy 2012). It enables the prediction of future changes in the genetic and demographic health of a population. We use pedigree simulations with realistic biological parameters derived from the Association of Zoos and Aquariums (AZA) Species Survival Plan for Arabian Oryx (AZA 2010) to assess the performance of GD retention and inbreeding avoidance by the 2 kinship-based strategies when pedigrees are uncertain. These 2 strategies are also compared with random mating and a nonkinship-based male rotation strategy, where a different breeding male is chosen at each timestep.

**Materials and Methods**

**Pedigree Simulation Overview**

Pedigrees were simulated to compare the effects of different management strategies on 2 summary statistics of the population, GD and average inbreeding (*F*). A captive population’s GD (or average expected heterozygosity) relative to the population’s founders is given as GD = 1 − MK, where MK is the average MK of all individuals in the population (Ballou and Lacy 1995). MKs are calculated for each individual as the average of pairwise kinship coefficients (f) between that individual and all living individuals in the population, including itself. MK is simply the average MK of all individuals in the population. An individual’s inbreeding coefficient (F) is the probability that the 2 homologous alleles at a locus are identical by descent, and it is equal to the f of that individual’s sire and dam. Algorithms for calculating traditional pedigree summary statistics and their extensions when pedigrees are unknown or uncertain are those used in the software program PMx (Ballou and Lacy 1995; Lacy 2012; Lacy et al. 2012).

Pedigrees were simulated with a forward-in-time approach starting with a group of either 30 or 100 unrelated founders. It should be noted that the median number of founders in cooperatively managed captive breeding programs within AZA is 15 (Long et al. 2011). However, using fewer than 20 founders resulted in a high proportion of simulated populations crashing (i.e., the population size declined to 0). Although optimistic, 30 founders were used as a realistic estimate for a captive population to retain >98% of the heterozygosity present in an outbred population (Frankham et al. 2002), and 100 founders were also simulated so that early rapid population growth to the target size of 100 individuals is not a confounding factor in GD and F estimates. The founders for each simulation were assigned ages based on a stable age distribution within the breeding age range (4–15 years) and an equal probability of male or female assignment. For each management strategy, 1000 simulations were performed. Every simulation ran for 100 timesteps, which is equivalent to 100 years as interbirth interval for female Arabian oryx is approximately 1 year in captivity in North America (Price, 1989). The demographic parameters of the simulations were derived from values typical of United States *ex situ* populations of Arabian oryx (Correll et al. 2010; Table 1), with the exception of the probability of each pair successfully producing offspring. In a captive setting, a pair may fail to produce an offspring owing to behavioral or medical issues. Probability of successful reproduction was chosen to be 0.80 based on estimates of the number of females of reproductive age and the number of offspring at 3 AZA institutions breeding the largest number of oryx over
were calculated and recorded.

The simulation program was written in C++ and is available by request. For most mammals, however, this estimate is likely to be much smaller. The simulation program was written in C++ and is available by request.

Simulation Steps

1. At the beginning of each timestep, the number of offspring needed to bring the population to the target size of 100 was estimated. This estimate accounted for the offspring (or first-year) mortality rate and the expected adult mortality of the existing population. The number of necessary breeding females was then estimated based on the probability of a mated pair successfully breeding and that only 1 offspring per female could be produced within each timestep.

2. Breeding pairs for the timestep were then chosen according to the breeding strategy being simulated (described in Kinship-Based Strategies and Non-MK Strategies) until the estimated number of new offspring needed was obtained. When it was not possible to reach the population target size, the maximum number of possible pairs were made. For all breeding strategies, the mating system included overlapping generations.

3. If a breeding pair successfully reproduced, 1 offspring was added to the population and assigned as male or female with 0.5 probability. Once all the new offspring were added, a pairwise f matrix was calculated for the population using algorithms described in Lacy (2012) and Lacy et al. (2012) for PMx software.

4. Adult and first-year mortality rates at the probabilities were estimated from the studbook and are listed in Table 1. These parameters were derived from values typical of United States ex situ populations of Arabian oryx. The past 5 years (San Diego Zoo Safari Park, Glady Porter Zoo, and Fossil Rim). For most mammals, however, this estimate is likely to be much smaller. The simulation program was written in C++ and is available by request.

**Table 1** Demographic parameters used in simulations

<table>
<thead>
<tr>
<th>Demographic parameters</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>First-year mortality rate</td>
<td>0.23</td>
</tr>
<tr>
<td>Adult mortality rate</td>
<td>0.05</td>
</tr>
<tr>
<td>Number of offspring per successful mating</td>
<td>1</td>
</tr>
<tr>
<td>Minimum reproductive age</td>
<td>4</td>
</tr>
<tr>
<td>Maximum reproductive age</td>
<td>15</td>
</tr>
<tr>
<td>Probability of reproducing</td>
<td>0.8</td>
</tr>
</tbody>
</table>

These parameters were derived from values typical of United States ex situ populations of Arabian oryx.

Kinship-Based Strategies: Unk and Mult

The mating system for the kinship-based strategies was monogamous and based on a static list of MKs that ranked individuals by their MK values at the beginning of each timestep (Ivy and Lacy 2012). At the start of each timestep, the MKs were calculated anew. The male and female with the lowest MK values were chosen to create a breeding pair. In captive population management, close inbreeding is avoided, thus males and females were accepted as a breeding pair if their f value was close to or less than the population’s MK. Individuals were bred without replacement; individuals chosen to breed were removed from the breeding pool for the remainder of the timestep.

For comparison, new offspring were modeled to have either a 10%, 25%, 50%, or 75% probability of having an unknown sire (Unk_sire) or multiple possible sires (Mult_sire). Simulations where both an offspring’s sire and dam may be unknown (Unk_sire/dam) or the occurrence of multiple possible sires and dams (Mult_sire/dam) were also performed with varying probabilities. For these models, after a male and female were chosen as a breeding pair, their offspring was assigned to have either their sire and/or dam (Unk_sire/dam, Mult_sire/dam) to be unknown or uncertain with 10%, 25%, 50%, or 75% probability depending on the scenario. For the Mult simulations, all sires (Mult_sire) or sires and dams (Mult_sire/dam) chosen to breed during a timestep became the group of potential parents for offspring with uncertain parentage within that timestep. Each parent within the group was given equal probability of being the true sire and/or dam. In addition to the Mult and Unk scenarios, control scenarios of 100% known pedigree were modeled to examine the long-term changes in GD and F under optimal conditions.

The f matrix of true and observed (Mult or Unk) relationships was kept track of simultaneously within each simulation scenario. Breeding pairs are chosen from the observed kinship matrix. However, the GD and F from the true matrix are reported in the Results section as those values represent the real outcome of the different strategies being tested.

Non-MK Strategies

Two nonkinship-based breeding strategies were also modeled for comparison with the kinship-based strategies. One strategy, referred to as Random, allowed breeding pairs to be chosen randomly. Within each timestep, males were chosen for breeding with replacement back into the breeding pool, but females were chosen without replacement.

The second nonkinship-based breeding strategy is referred to here as Dominant Male. Zoos often maintain Arabian oryx and other large antelopes in mixed-sex herds when maintaining bachelor/bachelorette herds are not logistically feasible. However, in Arabian oryx and many antelopes, a dominant male within a herd gets the most, but not all, breeding opportunities. In captivity, this can lead to a rapid increase in inbreeding and loss of genetic diversity without adequate population management. Few North American institutions have enough space to maintain separate bachelor and bachelorette herds plus an additional smaller breeding nucleus in order to better
control breeding. For the Dominant Male strategy, 1 male was randomly chosen at each timestep to breed with randomly chosen females until the desired number of offspring was reached. Once a male was chosen, he could not go back into the pool of potential breeders for the duration of his reproductive life. Removing a previously breeding male from the potentially breeding population is intended to represent a rotational breeding scheme that has been used in place of MK strategies, especially when pedigrees are unknown (Honda et al. 2004). Each female typically had the opportunity to breed with 6 different males as the average reproductive time span for females was ~6 years.

In both nonkinship-based breeding strategies, the pedigrees were completely known for all individuals, and the GD and \( F \) summary statistics were calculated using standard algorithms (Ballou and Lacy 1995). To compare GD and \( F \) averages across scenarios, 95% confidence intervals (CIs) were calculated from each set of 1000 simulations. Using a conservative approach, 2 scenarios were considered significantly different from one another if their 95% CI did not overlap (\( P < 0.05 \)).

**Results**

**Offspring with an Unknown Sire (Unk_sire) or Multiple Possible Sires (Mult_sire)**

Compared with the simulated population’s founders, simulations for which offspring were assigned multiple possible sires (Mult_sire) with 10%, 25%, 50%, or 75% probability retained an average of 94.2–94.5% GD with 100 founders and 92.5–92.9% with 30 founders after 100 timesteps (Figure 1). The mean \( F \) ranged from 3.5% to 3.8% with 100 founders and 5.1% to 5.9% with 30 founders after 100 timesteps (Figure 2). The retention of GD and avoidance of increased \( F \) were greater in Mult_sire than Unk_sire. The Unk_sire simulations retained 91.4–93.2% of initial GD with 100 founders and 89.6–91.6% with 30 founders after 100 timesteps (Figure 1). The mean \( F \) ranged from 4.5% to 6.6% with 100 founders and 6.2% to 8.5% with 30 founders (Figure 2). As expected for both the Mult_sire and Unk_sire scenarios, the greater the probability of an unknown or uncertain parent in the population, the larger the loss of GD and increase of \( F \) after 100 timesteps. For each scenario, mean GD and \( F \) and 95% CIs are reported in Supplementary Tables 1 and 2. Graphs illustrating the decay of GD and increase in \( F \) at each timestep are shown in Supplementary Figures 1 and 2.

When only 10% of new offspring were assigned an unknown sire (Unk_sire) at each timestep, there was significantly (\( P < 0.05 \)) greater \( F \) and less GD in the true pedigree after 100 timesteps compared to assigning 10% of offspring multiple possible sires (Mult_sire) (Figures 1 and 2). At each simulated probability of uncertain or unknown parentage in Mult_sire and Unk_sire scenarios, values of average GD and \( F \) were significantly different. The pattern of GD loss and increase in \( F \) over time was similar regardless of whether 30 or 100 unrelated founders began the pedigree simulations. Mult_sire consistently outperformed Unk_sire and the nonkinship-based breeding strategies (Random and Dominant_Male) performed significantly worse than all Mult_sire and Unk_sire scenarios. Within Mult_sire and Unk_sire scenarios and across varying probabilities of uncertainty, there were only a few significant differences in GD and \( F \). There is statistical significance (\( P < 0.05 \)) in GD between Unk_sire 10% and 75%, as well as 25% and 75% with both 30 and 100 founders (Supplementary Table 1). For \( F \), statistical significance between probabilities of uncertainty was only seen between 10% and 75% in Unk_sire with 30 and 100 founders (Supplementary Table 2).

**Offspring with Unknown Sires and/or Dams (Unk_sire/dam) or Multiple Possible Sires and/or Dams (Mult_sire/dam)**

In the Unk_sire/dam scenarios, \( F \) increased and GD decreased at a substantially faster rate than in the Mult_sire/dam scenarios. If both parents of an individual are assigned as being unknown, kinship and inbreeding coefficients cannot be defined. These individuals cannot be selected for breeding based on kinship and may contribute to a more rapid decline in GD and increase in \( F \) in the Unk_sire/dam strategies. Simulations in which offspring were assigned multiple possible sires and/or dams with 10%, 25%, 50%, or 75% probability retained an average of 94.2–94.5% GD with 100 founders and 92.1–92.2% with 30 founders after 100 years (Figure 1). \( F \) ranged from 4.8% to 4.9% with 100 founders and 6.5% to 6.6% with 30 founders (Figure 2). Similar to Mult_sire and Unk_sire, the retention of GD and avoidance of \( F \) were generally greater in Mult_sire/dam than Unk_sire/dam after 100 timesteps. The Unk_sire/dam scenarios retained 84.4–93.1% of initial GD with 100 founders and 81.2–91.5% with 30 founders (Figure 1). Mean \( F \) ranged from 4.7% to 14.2% with 100 founders and 6.3% to 17.4% with 30 founders (Figure 2). Average GD and mean \( F \) are listed in Supplementary Tables 1 and 2 with 95% CI.

After 100 timesteps, Mult_sire/dam strategies outperformed Unk_sire/dam in retaining GD and avoiding an increase in \( F \) with 2 exceptions. When 10% of offspring were assigned uncertain or unknown parentage, there was no significant difference between Mult_sire/dam and Unk_sire/dam strategies in GD and \( F \) for both 30 and 100 founders. Additionally, if 25% of offspring had uncertain or unknown parentage, \( F \) did not differ significantly between Mult_sire/dam and Unk_sire/dam strategies with 30 founders.

True values of GD and \( F \) are reported here to evaluate the performance of kinship-based strategies when various proportions of a pedigree are unknown or uncertain. The simulations also recorded the observed values of GD and \( F \). These are the values reported by PMx for a given scenario. The difference between the true and the observed values after 100 timesteps shows that as the percentage of unknown pedigree increases, the greater the increase of GD underestimation (Figure 3a,c). In the Mult_sire and Mult_sire/dam scenarios, increases in pedigree uncertainty did not affect the degree of difference between the observed and true values of GD, but they were consistently underestimated.
of $F$ in Unk_sire and Unk_sire/dam simulations underestimated the true amount of inbreeding (Figure 3b,d), and the discrepancy between the true and observed values increased as the proportion of unknown pedigree increased. In contrast, the Mult_sire and Mult_sire/dam scenarios overestimated the amount of inbreeding and did not appear to be sensitive to the proportion of uncertainty in the pedigree.

### Nonkinship-Based Management Strategies

Between the 2 nonkinship-based strategies, Random performed better than Dominant Male in GD and $F$ after 100 timesteps with both founder population sizes. The Random simulations retained an average GD of 87.9% (Figure 1) and an 11.3% increase in average $F$ (Figure 2) with 100 founders and retained 85.3% GD (Figure 1) and an increase of 14.0% $F$ with 30 founders (Figure 2).

The Mult scenarios significantly outperformed both the nonkinship breeding strategies for GD and $F$. Omitting the unknown portion of the pedigree (Unk_sire/dam) in 75% of the offspring at each timestep resulted in a significant increase in $F$ and loss of GD compared with the Random mating scenario with both 30 and 100 founders. However, Unk_sire/dam with 75% of offspring having unknown parentage outperformed, but was not significantly different from, the Dominant Male strategy in terms of GD and $F$ ($P > 0.05$).

The Dominant Male scenarios for 30 and 100 founders had the worst performance of any tested, likely owed to random choice of the timestep’s sire and the half-sib relationships between all offspring within that timestep. After 100 timesteps, the average GD of Dominant_Male was 80.5% (Figure 1) and $F$ was 17.5% (Figure 2) with 100 founders and 78.9% GD (Figure 1) and 20.6% $F$ (Figure 2) with 30 founders.

### Discussion

Pedigree simulations that use demographic parameters estimated from captive Arabian oryx show that for a given
percentage of uncertainty in parentage, a significantly greater retention of GD occurs when all potential sires and dams (Mult_sire and Mult_sire/dam) are recorded and used for kinship-based breeding compared with removing any unknown portion of the genome from kinship estimation (Unk_sire and Unk_sire/dam) (Figure 1). This pattern is also true for F, although to a lesser degree at low percentages of pedigree uncertainty. When ≤10% of offspring within a timestep have uncertain sires and dams, using Unk or Mult strategies does not result in a significant difference in F after 100 timesteps (equivalent to 100 years) when 100 unrelated founders begin the population. If only 30 founders begin the population, there is not a significant difference in F between Mult_sire and Unk_sire with ≤10% uncertainty and no significance between Mult_sire/dam and Unk_sire/dam with ≤25% uncertainty. In addition, the control scenario of 100% Known pedigree performs almost as well as all the Mult_sire scenarios when 30 and 100 founders begin the population.

The ability of Mult strategies to retain significantly more GD and avoid higher F than Unk, especially at 50% and 75% uncertainty of offspring parentage, can be attributed to several factors. MK under the Unk_sire strategy is only calculated using the known portion of an individual’s pedigree. If a sire of an offspring is unknown, then only the known genomic portion of the dam and all other members of the population will be used to calculate that offspring’s kinship coefficients (f). Thus, the offspring’s observed MK will not include its relationship with the true sire and the sire’s side of the pedigree. This could result in an under- or overestimation of the observed MK compared with the true MK and the potential for the offspring to be paired with a close relative for breeding.

An additional drawback of using the Unk strategy as implemented here occurs when both the sire and dam are unknown (i.e., Unk_sire/dam). In this case, the f of the sire and dam and F of their offspring cannot be calculated. The offspring are therefore removed from consideration as a potential sire or

Figure 2. Average values of observed inbreeding (F) after 100 timesteps for each scenario. (a) and (b) are simulations that begin with 100 founders, and (c) and (d) are simulations that begin with 30 founders. Probability of offspring having unknown (Unk) or uncertain (Mult) parentage is given in parentheses next to each scenario name.
dam, and the net effect is to reduce the effective population size \( (N_e; \text{Lacy 2012}) \). This in turn will increase the loss of GD and increase in \( F \) in the population over time.

Unlike the \textit{Unk} strategy, \textit{Multi} distributes the probabilities of parentage over a number of possible parents (Lacy 2012). The assignment of breeding pairs in our MK model considered the \( F \) of potential offspring (equivalent to the \( f \) of the sire and dam) to avoid close inbreeding. A potential sire and dam were only chosen to breed if their \( f \) was equal to or less than the population’s \( MK \). Thus, the greater the number of founders and the target population size, the easier it is to avoid breeding pairs that are potentially related based on the observed pedigree because any potentially related individuals will be ranked lower for breeding. Therefore, using a MK breeding strategy with \textit{Multi} results in a more conservative approach than \textit{Unk} relative to both average GD and \( F \).

A shortcoming of the \textit{Multi} strategy, however, is that the observed pedigree may assign a breeding pair a greater \( f \) than is reflected in the true pedigree because the pair was given some probability of relatedness when they were in fact not related, and a genetically well-suited pair will not be chosen to breed. The alternative to not using \textit{Multi} information, however, is the potential to select closely related animals to breed, which may be a less desirable outcome. In addition, the drawback of overestimating \( f \) appears to have minimal effect on average GD and \( F \) in our scenarios as there is little difference in those summary statistics across percentages of offspring having multiple possible parents (Figures 1 and 2). This small effect across percentages of uncertain parentage may result from the small number of potential parents within each timestep. Given the demographic parameters used in the simulations and the target size of 100 individuals, there was between 2 (for 10% probability of \textit{Multi} parentage) and 5 (for 75% probability of \textit{Multi} parentage) possible sires and/or dams for offspring chosen to have \textit{Multi} sires and/or dams. Although not examined here, the size of the pool of potential \textit{Multi} sires and dams would likely effect values of GD and \( F \) after many timesteps. For example, if all eligible sires and dams in a population were assigned as potential parents of the majority of offspring, the choice of breeding pairs based on MK may begin to look similar to random mating.

The true and observed values of GD and \( F \) after 100 timesteps were compared to evaluate if \textit{Unk} or \textit{Multi} scenarios consistently over- or underestimate these summary statistics. The simulations show that as the proportion of unknown pedigree increases, the ability to accurately estimate how far the population is from the true GD and \( F \) also decays (Figure 3). Interestingly, the \textit{Unk} scenarios underestimate the
loss of GD but also underestimate inbreeding in the population. The Mult scenarios similarly underestimate the loss of GD but overestimate inbreeding. Unlike the Unk scenarios, the Mult scenarios do not appear to be sensitive to the amount of uncertainty in the pedigree. Additional research is needed to identify how the number of individuals that make up the Mult affects GD and \( \bar{F} \). For example, if a large proportion of the breeding population is a potential parent, this may increase the rate of GD decay under certain circumstances such as a shallow pedigree with many founders.

The MK-based breeding strategies of Unk and Mult were also compared with nonkinship-based strategies that are often used in collections of large captive populations. The Mult strategies always outperformed the Random and Dominant Male scenarios for both GD and \( \bar{F} \). The only scenarios where a nonkinship-based strategy outperformed a kinship-based strategy after 100 timesteps was when there was a 75% probability that sires and dams of offspring were unknown (Unk sire/dam). In this case, the Random model retained an additional 3–4% of GD and avoided 3–4% of \( \bar{F} \) compared with Unk sire/dam in simulations with both 30 and 100 founders. This can be attributed to the markedly reduced \( N_e \) in Unk sire/dam observed pedigrees when the majority of a population's offspring have both an unknown sire and dam. The consistently poor performance of the Dominant Male strategy is owed to the half-sib relationship of all offspring produced within each timestep and the random choice of the breeding male for each timestep. A dominant male strategy that involves utilizing pedigree and/or kinship information would not have as poor of a performance as the nonkinship Dominant Male strategy used here, which randomly chose the breeding male for each timestep. This type of strategy is frequently used among institutions with cooperative breeding programs that rotate unrelated males between their large captive herds of antelope.

Given the demographic parameters of ex situ Arabian oryx, population management that incorporates all possible sires and dams will be better positioned to maintain GD and prevent inbreeding accumulation than if the unknown portion of an offspring's genome is completely omitted from kinship calculations. This is especially true if ≥25% of a population's offspring have unknown sires and dams. The model results reported here are specific to the Arabian oryx held within AZA institutions, although the trend of GD retention and increase in \( \bar{F} \) is expected to hold true for other large antelope species.

Molecular methods can also provide relatedness estimates in populations where individuals have incomplete pedigrees (Haig et al. 1994; Blouin et al. 1996; Jones et al. 2002; Russello and Amato 2004; Iyengar et al. 2007; Ivy et al. 2009; Gonçalves da Silva et al. 2010; Mitchell et al. 2011). Their utility, however, depends on several factors. A large number of markers are usually needed to decrease the high sampling variance of the relatedness estimators (Russello and Amato 2004; Santure et al. 2010). Other studies have found that unless the kinship among founders is very high, the molecular estimates may add little value (Rudnick and Lacy 2008; Ivy et al. 2009). Thus, utilizing pedigree-based algorithms in the software program PMx (Lacy et al. 2011) that calculate kinship coefficients based on multiple possible parents will be more feasible for many population managers than incorporating molecular data when resources for DNA-based analyses are scarce. Moreover, there are >500 species that are cooperatively managed among AZA institutions, and adequate molecular markers have not been developed for a majority of them.

Maximizing GD retention and avoiding inbreeding is increasingly important because across animal taxa, there is a high risk of unsustainability in captive populations (Lees and Wilcken 2009; Leus et al. 2011; Long et al. 2011). Difficulty in importing wild individuals and lack of dedicated space within institutions contributes to dwindling numbers, especially for antelopes (Fischer 2009). Although the proportion of threatened antelope species represented in zoos is large (Price et al. 2004), few are managed sustainably. Of the 36 captive antelope species that have active population management through the AZA, none are considered both demographically and genetically sustainable (www.aza.org). The majority of these antelopes do not meet the sustainability criteria of 90% GD retention over a period of 100 years or 10 generations. In part, this is because of the large degree of pedigree uncertainty within most populations, which has the potential to lose genetically valuable animals through lack of rigorous management. For the Arabian oryx and species with similar demographic parameters, breeding strategies that incorporate multiple potential parents can be used to improve genetic management. A study comparing breeding-pair selection strategies by Ivy and Lacy (2012) identified that generation length and the rate of breeding-pair success are demographic parameters that have a large impact on retaining GD and limiting \( \bar{F} \). Performance of the strategies tested here would benefit from varying these demographic parameters to determine their broader applicability.

**Supplementary Material**


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