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Incorporating drivers of reproductive success improves population viability analysis

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Abstract

Population viability analysis (PVA) utilizes simulation models to project the genetic and demographic trajectories of populations over time. One benefit to using PVA to assist in ex situ population planning is the ability to compare outcomes from multiple management scenarios. Reproductive viability analysis (RVA), used to identify biological and reproductive characteristics of animals in breeding pairs that correlate with successful reproduction, is also beneficial, informing population managers on best practices for population planning. Our objectives were to: (1) compare genetic and demographic predictions for the managed North American ex situ fennec fox population from two PVA programs: Vortex and ZooRisk; (2) show how RVA results can be incorporated into PVAs in Vortex and how that affects PVA projections; and (3) perform a sensitivity analysis to investigate how uncertainty in the influence of factors on the reproductive success of fennec fox pairs affects variation in population projections. In this study, the relative and average genetic and demographic predictions were generally the same across both software programs when given similar inputs. The inclusion of factors that influence breeding success (RVA) in the PVA models resulted in a lower probability of extinction, less inbreeding accumulation, and slower loss of genetic diversity, due to an overall higher rate of reproductive success. The uncertainty in the negative effects of increasing female and male age, and the positive effect of female parity on reproductive success had the greatest effect on projected genetic diversity and inbreeding. Our study demonstrates that Vortex is capable of projecting the viability of ex situ populations with flexibility, and has the ability to incorporate complexity and uncertainty into population parameters. It also reveals that adjusting ex situ population management, more specifically the consideration of factors affecting reproductive success to create breeding pairs with a higher probability of success, will improve population sustainability.

Introduction

Accredited zoos and aquariums strive to maintain animal populations for the long term so that those populations can support conservation, education, research, and recreational goals (Traylor-Holzer, Leus, & Byers, 2018; Powell, Dorsey, & Faust, 2019), but analyses have revealed that many populations of animals managed in human care are not sustainable (Lees & Wilcken, 2009) and struggle with unexplained low or inconsistent rates of reproduction (Long, Dorsey, & Boyle, 2011; Faust *et al.*, 2019). The Association of Zoos and Aquariums' (AZA) Reproductive Management Center has developed reproductive viability analysis (RVA) as a tool to identify the inherent biological and reproductive characteristics of animals in breeding pairs and the pairs themselves that correlate with successful reproduction in order to inform population managers on best practices for population management and to improve genetic and demographic predictions. The RVA process identifies predictors of reproductive success based on past performance of breeding pairs using a regression model of reproductive success against multiple individual and breeding pair attributes. This provides the opportunity to link the results from an RVA with population viability analyses: the PVA uses the regression parameters to predict the reproductive success of current and new breeding pairs (Bauman *et al*., 2019; see “Methods” section for more details). Modeling population genetic and demographic status under management scenarios that are informed by RVA makes it possible to develop models for how to manage individual animals throughout their lives tha maximize their own reproduction and the population’s viability.

Population viability analysis (PVA) is a quantitative analysis utilizing simulation models to project the genetic and demographic trajectories of populations over time (Lacy, 1993; Beissinger & Westphal, 1998; Beissinger, 2002). PVA expands upon traditional demographic analyses that project population growth from mean age-specific birth and death rates (Caswell, 2001) by incorporating stochasticity in demographic, environmental and genetic processes (Shaffer, 1981) and considering the interactions among threats that can cause population instability and lead to rapid extinction (Gilpin & Soulé, 1986; Lacy, 2000a). Projections of ex situ populations have until recently focused on mean trajectories calculated by deterministic analysis of demography and genetics as separate processes (Ballou *et al*., 2010). Although originally developed to assess threats to in situ population sustainability, PVAs can also be useful for the long-term management of ex situ populations (Lacy, 2019). Moreover, the detailed demographic and pedigree data available for many managed ex situ populations allow for more accurate estimation of the input parameters necessary for PVA, minimizing the risk of inadequate data that often hinders reliable population projections for most in situ populations (Ralls, Beissinger, & Cochrane, 2002). One of the benefits to using PVA as a tool to assist in ex situ population planning is the ability to run multiple management scenarios that project a range of possible outcomes, as has been completed for over 100 cooperative breeding programs in North America (Che-Castaldo *et al*., 2019).

Currently, the management of animals in zoos accredited by the AZA (and many other regional zoo associations) involves the development of breeding and transfer recommendations every 1 to 3 years based on the present genetic value of individuals and the demographic needs of the population. Typically, the desired impact of these breeding and transfer recommendations are to maintain a stable or growing population and minimize the loss of genetic diversity (Ballou & Lacy, 1995; Montgomery *et al*., 1997; Rodriguez-Clark, 1999) in order to meet longer-term program goals. Some ex situ programs have incorporated PVA into their population planning process. For example, multiple programs have evaluated the risk to the sustainability of the ex situ population associated with supplementation of wild populations (Bustamante, 1996; Zeoli, Sayler, & Wielgus, 2008; Earnhardt, Thompson, & Faust, 2009).

Incorporation of the results from an RVA into a PVA for ex situ population management will allow managers to adjust their recommendations based on the probability of breeding success for each pair, which should help them to better meet demographic targets and maximize reproductive success for genetically valuable priority breeders. The cooperatively managed AZA Species Survival Plan® (SSP) North American ex situ fennec fox (*Vulpes zerda)* population provides a novel opportunity to investigate how the integration of the results from an RVA into PVA models may affect genetic and demographic projections, since both a PVA and an RVA have recently been completed for this population.

In this study, we show how the results from the fennec fox RVA can be incorporated into the PVA using Vortex, and we explore how its incorporation affects population viability projections. As a preliminary step to our investigation, we first compare the population predictions for the fennec fox SSP population in Vortex (Lacy & Pollak, 2017), originally designed for in situ populations (Lacy, 1993, 2000b), to predictions from ZooRisk (Earnhardt *et al*., 2008), the software program developed for analysis of managed ex situ populations, which has been used for PVA modeling of SSP populations most frequently (Che-Castaldo *et al*., 2019). Additionally, an important component of PVA is sensitivity analysis, which assesses the impact of uncertainty in model parameters on the projected outcomes (Ludwig, 1996; Saether & Engen, 2002; McGowan, Runge, & Larson, 2011). This allows the identification of those inputs to which population projections are most sensitive, indicating the value of targeted research for more accurate estimation of those parameters and highlighting their importance for management (Moore *et al*., 2012). Therefore, in this study, we also performed a sensitivity analysis to investigate how our uncertainty in the influence of certain factors on the reproductive success of fennec fox pairs affects population projections.

Materials and methods

Study Species

Native to the North African Sahara, the fennec fox (*V. zerda)* is the smallest canid in the world. There is a paucity of data from the wild, which hampers conservation efforts (Bauman *et al*., 2010; IUCN, 2020). The majority of our knowledge for this species stems from studies of the ex situ population (Valdespino, Asa, & Bauman, 2002; Asa & Valdespino, 2003; Mekarska, 2006; Dempsey *et al*., 2009). All fennec foxes at AZA facilities are managed through the SSP, regardless of their respective roles (i.e. education, breeding or exhibition). A third of the fennec fox population is dedicated to educational roles and is one of the few carnivore species available for this purpose. In 2016, there were 131 total individuals (75 males, 56 females) located across 45 SSP facilities (Bauman, Knobbe, & Ivy, 2016).

Fennec foxes are sexually mature by 1 year of age. They are bred in pairs and typically have one litter a year; however, up to three litters within a 12-month period are possible if previous litters do not survive or kits are pulled for hand rearing. Litter size ranges from one to five kits (Valdespino *et al*., 2002). While stillborn kits are rare, neonatal mortality is fairly high but can be mitigated with successful hand rearing protocols. The greatest management challenge for the fennec fox SSP is inconsistent reproduction, causing boom-bust population cycles (average λ: 1962-1996 = 1.06;

1997-2009 = 0.95; 2010-2016 = 1.11; Bauman *et al.*, 2019, J. Ivy unpublished data). The fact that females do not reproduce after age 6 (Bauman *et al.*, 2019), despite a median life expectancy in both sexes of 11 years (Bauman, Clark, & Ivy, 2017), further compounds the problem. The fennec fox SSP population is vulnerable to extinction, if reproductive success does not improve (Johnson & Bauman, 2017).

Population viability analysis in Vortex 10

Twelve PVA scenarios for the fennec fox SSP population were evaluated using Vortex 10 (Lacy & Pollak, 2017). These scenarios were chosen to replicate the 12 scenarios evaluated from a previously completed PVA (Johnson & Bauman, 2017) in ZooRisk 3.8 (Earnhardt *et al.*, 2008). The model scenarios were originally designed in ZooRisk to reflect current management of the population, as well as potential alternative management strategies (Johnson & Bauman, 2017). Efforts were made to match Vortex model inputs and structure as closely as possible to those used in the ZooRisk model (Table S1) as a means to cross-check our PVA models. Scenario-specific parameters were: open versus closed population, duration of female reproductive lifespan, probability of breeding success and target (maximum) population size (Table 1). In the ZooRisk PVAs, open populations had 10 imports and 5 exports in year 5 of each decade, consisting of an even number of males and females ages 0-4. Imports were always considered "founders"; they were unrelated to one another and to the individuals in the SSP population. To simulate this as closely as possible in Vortex, we first created a separate population of "potential imports" generated through supplementation of 10 age = 1 individuals each year (five males and five females), with mortality = 100% at age 5. Worth noting, by default, Vortex normally starts each year just before the annual breeding season, so that the youngest individuals at the time of supplementation are age 1, which is why there were no age = 0 individuals in our population of potential imports. Therefore, in year 5 of every decade, this population contained 40 individuals, age 1 to 4. At this time, through dispersal, 25% of this population was moved into the SSP population (individuals chosen at random). Exports were simulated through the random harvest of 2.5 males and 2.5 females (age < 5) from the SSP in year 5 of every decade. Other model parameters and demographic rates did not vary between scenarios (Table S1).

Breeding pairs were selected based on the male's and female's genetic value using a static mean kinship list (i.e. the genetic value of individuals is not adjusted iteratively to account for likely reproduction by other breeding pairs selected at the same time; Ivy & Lacy, 2012). Population size was controlled in the model through limiting the number of breeding pairs each year (Breed to K option). The population was allowed to overshoot K (i.e. no truncation to K), with a breeding moratorium imposed in years when population size (N)> target population size (K). Populations at the start of the scenarios were initiated from studbook data and included the age, sex, rearing type, and parentage of each individual living in the ex situ population as of December 29th 2015. The starting studbook population had 159 (88 males and 71 females) total individuals (N_0), gene diversity (GD_0) of 93.8%, and a mean inbreeding (F_0) of 0.023 (Johnson & Bauman, 2017). No inbreeding depression effects were included in either the ZooRisk or Vortex models. Although reduced fitness of inbred animals is expected, ZooRisk and Vortex model inbreeding depression in different ways, and since the ZooRisk PVA did not incorporate inbreeding depression, we chose not to incorporate it into the Vortex PVA for consistency.

Projected population size (N_{100}), genetic diversity (GD_{100}), inbreeding accumulation (F_{100}), and the probability of extinction ($p(E)_{100}$) in year 100 were compared between the Vortex models and the previously published ZooRisk models using a predictive linear regression model in SAS Studio 3.7 (SAS Institute Inc., Cary, NC, USA). Population projections from ZooRisk were used as the predictive variable, and the Vortex model predictions were used as the response variable. The hypothesis tested was for the slope of the relationship between the two sets of models. A slope ($\beta 1$) equal to 1 would indicate similar relative performance of the models across both programs. Average values for projected N_{100}, GD_{100}, and F_{100} were also compared between ZooRisk and Vortex models using paired t-tests of the scenario results. The average ranks for $p(E)_{100}$ were compared using a Friedman's two-way nonparametric ANOVA. Significant differences were declared when $P < 0.05$.

Fennec fox reproductive viability analysis

The least absolute shrinkage and selection operator (LASSO) regression technique described in Bauman *et al.* (2019) was used to determine which attributes of fennec fox individuals and pairs drive reproductive success in the fennec fox SSP population. LASSO is a method of model selection that restricts the complexity of the model to prevent overfitting the data. For our analysis, we used the same dataset that was used for the original RVA completed for this population (Bauman *et al.*, 2019), in addition to data from the 2015 SSP Breeding and Transfer Plan (Bauman, Knobbe, & Ivy, 2015), as well as interim recommendations made in 2016, resulting in 17 additional breeding pairs being included in the analysis. The final dataset included a total of 148 fennec fox pairs given the opportunity to breed for at least 1 year. Although data for recommended pairs that were not given the opportunity to breed are valuable for exploration of logistical failures, they were not included in the RVA, which focuses on biological traits.

Reproductive success was defined as the production of offspring (including stillborn offspring) during the associated SSP Breeding and Transfer Plan period (see Bauman *et al.*, 2019 for details). Stillbirths were included in the RVA because the production of offspring carried to term, although dying in the peri-parturition period, still indicates that both partners were fertile and behaviorally compatible for mating. Because stillbirths may also be the result of external factors that are not inherent biological characteristics of the breeding

Table 1 The demographic input parameters for the Vortex models used for the PVA of the North American ex situ fennec fox population, where p(B) is the probability of breeding success for females, and TPS is the target population size

Scenario name	Population type	Female breeding ages	p(B)	TPS	Imports per decade	Exports per decade
Baseline scenarios						
(A) O-R10-pB25-K175	Open	1–10 years	25%	175	10	5
(B) C-R10-pB25-K175	Closed	1–10 years	25%	175	0	0
Alternative Scenarios: Lower Probability of Breeding Success for All Females						
(C) O-R10-pB18-K175	Open	1–10 years	18%	175	10	5
(D) O-R10-pB11.6-K175	Open	1–10 years	11.6%	175	10	5
Alternative Scenarios: Shorter Reproductive Lifespan for Females						
(E) O-R6-pB25-K175	Open	1–6 years	25%	175	10	5
(F) C-R6-pB25-K175	Closed	1–6 years	25%	175	0	0
(G) O-R6-pB31-K175	Open	1–6 years	31%	175	10	5
(H) C-R6-pB31-K175	Closed	1–6 years	31%	175	0	0
Alternative Scenarios: Reduced Space (Smaller Target Population Size)						
(I) O-R10-pB25-K150	Open	1–10 years	25%	150	10	5
(J) C-R10-pB25-K150	Closed	1–10 years	25%	150	0	0
(K) O-R10-pB25-K100	Open	1–10 years	25%	100	10	5
(L) C-R10-pB25-K100	Closed	1–10 years	25%	100	0	0

Underlined portions of the scenario name indicate where the scenario differs from the baseline scenario.

pair members (e.g. infectious agents), we did not penalize breeding pairs in the RVA when a stillbirth was recorded.

Variables used in the original RVA included: age of each individual, age difference between the male and female, similarity in male and female rearing types, reproductive history of both individuals with each other and with other mates, recent institution breeding success with the species, and whether both foxes were at the breeding location at the time the recommendation was made (see Bauman *et al.*, 2019 for details). The RVA was repeated for this study in order to include additional variables that were not included in the original analysis including individual parity (parous or nulliparous), individual rearing type (hand or parent reared), and prior history of contraception for the female (yes or no). Since the regression technique used is sensitive to the scale of the input variables, female age, male age, and the age difference between the male and female were standardized prior to analysis (by subtracting the mean and dividing by 2 standard deviations) in order to be compatible with the other binary inputs (Gelman, 2007). Seven different iterations of the RVA were completed such that each iteration used a different subset of the Breeding and Transfer Plans as the training versus testing data sets. The seven iterations were chosen by incrementally leaving out 2-3 consecutive B&T plan years for testing the models (refer to Table 3 for details). Performance of each iteration was measured using the area under the receiver operating characteristic (ROC) curve (AUC) for comparison to each other and the original RVA performed in Bauman *et al.*, 2019 as described therein.

Incorporation of the RVA results into the PVA

Incorporation of the results from the fennec fox RVA into the Vortex PVA was done using a complex function for determining the probability of a female not producing a litter, replacing the percentage assigned for each scenario from Table 1. The function for the probability of a female not producing a litter used was as follows:

$$100 \times \left(1 - \left(\frac{1}{1 + e^{-[\mathrm{RVA}]}}\right)\right),$$

where

$$\begin{aligned}\mathrm{RVA} = {} & (\mathrm{FPC} \times \mathrm{FP}) + (\mathrm{PPC} \times \mathrm{FP} \times \mathrm{MP}) \\ & + \left(\mathrm{MAC} \times \left[\left(\frac{\mathrm{MA} - 4.7692}{2 \times 3.616}\right)\right]\right) \\ & + \left(\mathrm{FAC} \times \left[\left(\frac{\mathrm{FA} - 4.4308}{2 \times 2.9635}\right)\right]\right) \\ & + \left(\mathrm{DAC} \times \left[\left(\frac{|\mathrm{MA} - \mathrm{FA}| - 2.6667}{2 \times 2.453}\right)\right]\right) \\ & + (\mathrm{EPC} \times \mathrm{EP}) + (\mathrm{HRC} \times \mathrm{PHR}) + (\mathrm{MRC} \times \mathrm{PMR}),\end{aligned}$$

and FPC is the female parity coefficient, PPC is the pair parity coefficient, $\mathrm{FP} = 1$ for females who have produced offspring before, $\mathrm{FP} = 0$ for nulliparous females, $\mathrm{MP} = 1$ for males who sired offspring before, $\mathrm{MP} = 0$ for nulliparous males, MAC is the male age coefficient, MA = male age, FAC is the female age coefficient, FA = female age, DAC is the age difference coefficient, EPC is the experienced pair coefficient, $\mathrm{EP} = 1$ for pairs who have successfully produced offspring together before, $\mathrm{EP} = 0$ for pairs who have not produced offspring together before, HRC is the hand-reared rearing type coefficient, $\mathrm{PHR} = 1$ when both the male and female were hand reared, $\mathrm{PHR} = 0$ when only one member of the pair or neither the male or female were hand reared, MRC is the mixed-reared rearing type coefficient, $\mathrm{PMR} = 1$ when the male and female have different rearing types and $\mathrm{PMR} = 0$ when the male and female have the same rearing

Table 2 Comparison of the average population projections (±SD) across 1000 iterations for population size (N), genetic diversity (GD), inbreeding accumulation (F) and the probability of extinction (p(E)) in year 100 for each PVA scenario of the North American ex situ fennec fox population evaluated in Vortex 10 and ZooRisk. Projections after incorporation of the RVA results are also presented (shaded)

Scenario name	Vortex 10				ZooRisk			
	N_{100}	GD_{100} (%)	F_{100}	$p(E)_{100}$ (%)	N_{100}	GD_{100} (%)	F_{100}	$p(E)_{100}$ (%)
Baseline scenarios								
(A) O-R10-pB25-K175	175 ± 7	97.1 ± 0.4	0.038 ± 0.020	0	175 ± 7	96.2 ± 0.5	0.056 ± 0.014	0
(B) C-R10-pB25-K175	176 ± 7	87.8 ± 0.6	0.124 ± 0.044	0	174 ± 7	87.2 ± 0.6	0.135 ± 0.013	0
(M) O-R10-RVA-K175	176 ± 6	97.7 ± 0.3	0.031 ± 0.018	0				
(N) C-R10-RVA-K175	177 ± 6	89.8 ± 0.6	0.109 ± 0.038	0				
Alternative scenarios:lower probability of breeding success for all females								
(C) O-R10-pB18-K175	166 ± 18	95.4 ± 1.0	0.062 ± 0.029	0	166 ± 15	94.4 ± 1.1	0.080 ± 0.020	0
(D) O-R10-pB11.6-K175	10 ± 9	86.5 ± 9.6	0.017 ± 0.053	2.4	11 ± 7	77.3 ± 14.7	0.039 ± 0.062	8
Alternative scenarios: shorter reproductive lifespan for females								
(E) O-R6-pB25-K175	144 ± 42	94.8 ± 2.3	0.050 ± 0.035	0	148 ± 35	94.4 ± 2.1	0.057 ± 0.019	0
(F) C-R6-pB25-K175	115 ± 65	76.2 ± 8.5	0.228 ± 0.136	14.5	130 ± 48	77.8 ± 7.5	0.209 ± 0.065	9
(G) O-R6-pB31-K175	175 ± 10	96.5 ± 0.5	0.035 ± 0.021	0	171 ± 11	95.7 ± 0.6	0.045 ± 0.012	0
(H) C-R6-pB31-K175	173 ± 16	84.3 ± 1.1	0.150 ± 0.058	0.4	171 ± 11	84.3 ± 0.8	0.150 ± 0.010	0
(O) O-R6-RVA-K175	178 ± 6	97.4 ± 0.3	0.026 ± 0.017	0				
(P) C-R6-RVA-K175	178 ± 6	87.4 ± 0.5	0.120 ± 0.045	0				
Alternative scenarios: reduced space (smaller target population size)								
(I) O-R10-pB25-K150	151 ± 7	96.8 ± 0.4	0.039 ± 0.022	0	149 ± 7	95.9 ± 0.6	0.058 ± 0.016	0
(J) C-R10-pB25-K150	150 ± 7	86.3 ± 0.6	0.138 ± 0.047	0	149 ± 7	85.8 ± 0.7	0.149 ± 0.015	0
(K) O-R10-pB25-K100	100 ± 6	96.2 ± 0.6	0.042 ± 0.027	0	99 ± 6	95.0 ± 0.8	0.061 ± 0.020	0
(L) C-R10-pB25-K100	99 ± 9	78.9 ± 3.1	0.211 ± 0.087	0.4	99 ± 6	81.1 ± 1.1	0.194 ± 0.020	0
(Q) O-R10-RVA-K150	151 ± 6	97.6 ± 0.3	0.031 ± 0.019	0				
(R) C-R10-RVA-K150	151 ± 5	88.5 ± 0.7	0.121 ± 0.043	0				
(S) O-R10-RVA-K100	101 ± 5	97.0 ± 0.4	0.031 ± 0.024	0				
(T) C-R10-RVA-K100	101 ± 5	83.1 ± 1.4	0.177 ± 0.068	0				
Alternative scenarios: reduced space with informed management								
(U) O-R10-RVA-K150-IM	152 ± 5	97.6 ± 0.3	0.028 ± 0.017	0				
(V) C-R10-RVA-K150-IM	152 ± 6	88.6 ± 0.7	0.120 ± 0.042	0				

Underlined portions of the scenario name indicate where the scenario differs from the baseline scenario.

type. Age variables were standardized prior to inclusion in the RVA, thus, numerical coefficients are used to convert male age, female age, and the pair's age difference in Vortex to align with the RVA input variables. For the starting population, rearing types for each individual were taken from the studbook. For new individuals, rearing type was randomly assigned at birth, with a 15% probability of being designated as hand reared. If both of an individual's parents were over 5 years of age, an animal was automatically designated as hand reared (in accord with management practices for the species).

Due to uncertainty in the magnitude of the effect on reproductive success of each of the factors included in the function (i.e. the variability among different iterations of the RVA), global state variables in Vortex were used to sample the regression coefficients used, resampling between PVA iterations, but held constant across all 100 years of a given iteration. For each PVA iteration, a coefficient was chosen for each factor randomly from a normal distribution defined by the mean and standard deviation presented for each factor (refer to RVA results Table 3). For factors that were not significant across all seven iterations of the RVA, a non-zero coefficient was chosen only for a subset of iterations, the number of which was determined based on the percentage of RVA iterations with a significant effect (e.g. only 28.57% of iterations were assigned a non-zero coefficient for the effect of mixed pair rearing type; refer to results Table 3). Additionally, values were constrained, such that a negative coefficient would not be assigned for a factor with a distribution around a positive mean (e.g. there could not be a negative effect of females having offspring previously). If a negative value was drawn, a coefficient of zero was used.

Projected N_{100}, GD_{100} and F_{100} were compared between the Vortex PVA models with and without incorporation of the RVA results using a predictive linear regression model in SAS Studio 3.7 (SAS Institute Inc., Cary, NC, USA). The population projections from the initial Vortex PVA models were used as the predictive variable, and the Vortex models incorporating the RVA results were used as the response variable. The hypothesis tested were the same as the previous set of comparisons. Significant differences were declared when $P < 0.05$.

In addition to using a complex function for determining an individual female's probability of reproductive success, we evaluated two additional scenarios in which we incorporated information learned from the RVA in Bauman *et al.* (2019) into the management strategy of the population. "Informed management" consisted of: (1) 90% of pairs being split after being together more than 2 years with no resulting litter production; and (2) criterion was added such that a female had an 80% probability of being paired with a male of the same rearing type.

Sensitivity analysis

Data from all 1000 iterations for four of the PVA scenarios (4000 total iterations) were used to investigate how the uncertainty in the magnitude of the effect for each factor contributing to a female's probability of success affected the resulting PVA projections. In order to also measure the influence of both population type (open vs. closed) and management strategy (status quo "traditional" vs. informed management) on demographic and genetic outcomes, the results from four scenarios representing these factors paired in all combinations were used for the sensitivity analysis (Q, R, U, and V in Table 2). Genetic and demographic outcomes investigated (dependent variables) included GD_{100}, F_{100}, number of breeding pairs needed per year to achieve the target population size of 150 (averaged across years), and the average proportion (across years) of breeding pairs that produced a litter within a given year ($p(B)_{avg}$). The data were analyzed in SAS® Studio 3.7 (SAS Institute Inc., Cary, NC, USA) using generalized linear models where fixed explanatory factors included population type, management strategy, and the population type x management strategy interaction term, and quantitative factors included the FPC, PPC, MAC, FAC, DAC, EPC, HRC, and MRC coefficients. The F test was used to declare a factor as explaining a significant amount of variability when $P < 0.05$. The ratio of the Type III sums of squares over the total sums of squares was used to calculate the percent of variation explained by the factor. Due to the majority of the variability in the datasets being attributable to population type (98.5% for GD_{100}, 66.0% for F_{100}, 30.2% for number of breeding pairs, and 30.5% for $p(B)_{avg}$), the sensitivity analyses were re-run separately for each population type, open and closed (2000 iterations each), in order to look more specifically at the factors contributing to a female's probability of reproductive success. Therefore, population type and the population type x management strategy interaction term were removed from the final models. Differences were declared when $P < 0.05$.

Results

Population viability analysis in vortex 10

Average population projections across iterations for N_{100}, GD_{100}, F_{100}, and $p(E)_{100}$ for each scenario from both Vortex 10 (this study) and ZooRisk (Johnson & Bauman, 2017) analyses are presented in Table 2. Relative projections from the 12 PVA scenarios were similar across both the ZooRisk and Vortex analyses for N_{100}, GD_{100}, and $p(E)_{100}$ (Figure 1). Similarly, the average values of N_{100} and GD_{100}, as well as the average ranks of $p(E)_{100}$ were not different between the two software programs ($\bar{x}_{diff} = 0.67$, $\bar{x}_{diff} = -0.01$, and $\bar{x}_{diff} = -1.67$, respectively). Although the effect is small, projected F varied more among scenarios using Vortex compared to ZooRisk ($B1 = 1.19$, H0: $\beta 1 = 1$, $P = 0.0004$, Figure 1C). Vortex scenarios for open populations projected lower F than did ZooRisk because Vortex includes the non-inbred imports in the calculations of mean inbreeding, whereas ZooRisk excludes new potential founders from the genetic tallies.

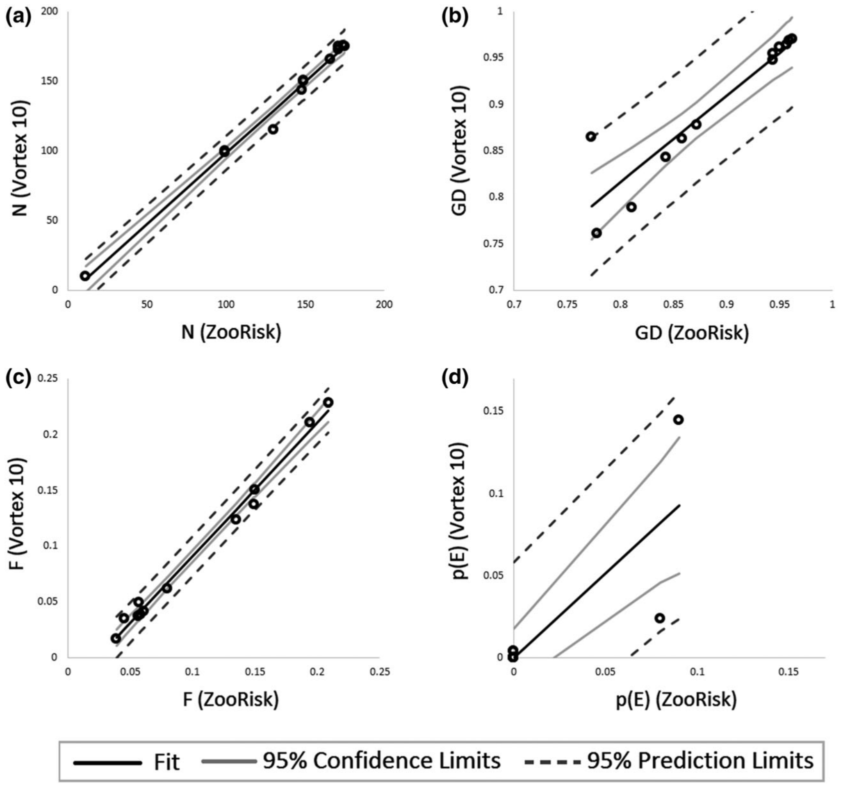

Figure 1 Relative average population projections for (a) population size, N, in year 100, (b) genetic diversity, GD, in year 100, (c) inbreeding accumulation, F, in year 100, and (d) the probability of population extinction, p(E), by year 100 for 12 PVA scenarios of the North American ex situ fennec fox population evaluated in both ZooRisk and Vortex 10.

Factors driving reproductive success in the ex situ fennec fox population

The results for each iteration of the fennec fox RVA are presented in Table 3. Across all seven iterations of the analysis (using different subsets as training vs. testing data sets), as female and/or male age increase, the probability of reproductive success of the pair decreases. Additionally, across all iterations, pairs in which both the male and female have previously produced offspring (pair parity = Yes/Yes) had a higher probability of reproductive success. These results are similar to the original RVA completed for this population (Bauman *et al*., 2019). Other effects were also found to be significant among a subset of the iterations. Six (85.7%) iterations found a positive influence of female parity (parous) on the reproductive success of the pair in addition to the effect of pair parity. Two (28.6%) iterations found a negative effect of mixed pair rearing type (hand reared individual paired with parent reared individual) on reproductive success. A negative effect of increasing age difference between the male and female, a positive effect of experienced pair types and a positive effect of both individuals in the pair being hand reared were each found in a single iteration (Iteration 1; Table 3). The AUC of the ROC across all iterations was 0.8423 ± 0.055 (mean ± standard deviation). Thus, the performance of these iterations was consistent with the original RVA (0.8304).

Incorporation of the RVA results into the Vortex PVA

Eight scenarios were evaluated that incorporated the RVA results into the Vortex PVA models by replacing the fixed probability of breeding with a pair-specific probability. This resulted in eight scenarios in lieu of the original 12, as several scenarios differed only by p(B) (i.e. scenarios A, C and D; scenarios E and G; scenarios F and H) (Table 1). Two additional scenarios not only incorporated RVA results but also used an “informed management” strategy as described in the methods. The resulting 100-year population projections for these 10 scenarios are presented in Table 2. The average annual proportion of females that reproduced successfully ($p(B)_{avg}$) and the number of pairs needed per year to breed to the target population size are presented in Table 4.

The inclusion of factors that influence breeding success (RVA) in the PVA model resulted in lower probabilities of extinction, lower accumulation of inbreeding, and slower loss of genetic variation. The $p(B)_{avg}$ ranged between 48.9 and 58.3 % among the RVA-based scenarios, which is substantially higher than p(B) used in scenarios in the original PVA models (11.6-31 %). There were no iterations among any scenario in which the population went extinct among the RVA-based scenarios. This is in contrast to two complementary scenarios, F (vs. P) and L (vs. T), which had p

Table 3 Iteration summaries including the LASSO coefficients[b] resulting from 7 iterations of the North American ex situ fennec fox population reproductive viability analysis. HR = Hand reared. NT = Not included in the analysis

ITERATION	1	2	3	4	5	6	7				
Training Data (years)	2004-2013	2004-2012 2015-2016	2004-2011 2014-2016	2004-2010 2013-2016	2004-2009 2012-2016	2004-2006 2011-2016	2004, 2010-2016			Iterations with Significant Effect (%)	Bauman *et al.*, 2019
Testing Data (years)	2014-2016	2013-2014	2012-2013	2011-2012	2010-2011	2008-2010	2006-2008	Mean[a]	SD		
AUC of the ROC	0.7886	0.8581	0.8435	0.8327	0.7615	0.9020	0.9098	0.8423	0.0546		0.8304
LASSO Coefficients											
Female Age	−1.345	−0.977	−0.205	−0.465	−0.979	−1.029	−0.629	−0.8041	0.3892	100	−0.289
Male Age	−0.380	−1.031	−0.613	−0.549	−0.515	−0.665	−0.570	−0.6174	0.2031	100	−0.241
Age Difference	−0.257	0.000	0.000	0.000	0.000	0.000	0.000	−0.2566	–	14.29	0.000
Pair Type: Carryover	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	0.000
Pair Type: Experienced	0.079	0.000	0.000	0.000	0.000	0.000	0.000	0.0789	–	14.29	0.461
Pair Rearing Type: HR	0.133	0.000	0.000	0.000	0.000	0.000	0.000	0.1331	–	14.29	0.000
Pair Rearing Type: Mixed	−0.489	0.000	0.000	0.000	0.000	0.000	−0.147	−0.3176	0.2420	28.57	0.000
Female Rearing Type: HR	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	NT
Male Rearing Type: HR	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	NT
Pair Parity: Yes/Yes	0.894	0.638	0.004	0.061	0.639	0.921	0.797	0.5649	0.3804	100	0.000
Pair Parity: Mixed	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	0.000
Female Parity: Yes	0.000	0.506	0.123	0.401	0.608	0.716	0.742	0.5161	0.2313	85.71	NT
Male Parity: Yes	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	NT
Female has prior history of contraception	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	NT
Institutional success during last 5 years	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	0.000
Institutional success during last 10 years	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	0.000
Both at breeding location: Yes	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–	0	0.000

[a] Calculation of mean does not include non–significant coefficients (values of 0.000).

[b] There are no coefficients for reference levels of each factor.

Table 4 Average proportion of females that were reproductively successful per year ($p(B)_{avg}$) and the number of pairs needed per year (on average) to breed to the target population size ±SD for each PVA scenario of the North American ex situ fennec fox population evaluated in Vortex 10 after incorporation of the RVA

Scenario Name	Aligns to original scenario(s):	$p(B)_{avg}$ (%)	Breeding Pairs (avg/year)
Baseline Scenarios			
(M) O-R10-RVA-K175	A,C,D	53.9 ± 3.9	21 ± 2
(N) C-R10-RVA-K175	B	48.9 ± 4.0	23 ± 2
Alternative Scenarios: Shorter Reproductive Lifespan for Females			
(O) O-R6-RVA-K175	E,G	58.3 ± 3.7	20 ± 1
(P) C-R6-RVA-K175	F,H	54.9 ± 3.4	21 ± 1
Alternative Scenarios: Reduced Space (Smaller Target Population Size)			
(Q) O-R10-RVA-K150	I	54.2 ± 3.9	18 ± 1
(R) C-R10-RVA-K150	J	49.0 ± 4.0	20 ± 2
(S) O-R10-RVA-K100	K	54.8 ± 3.9	12 ± 1
(T) C-R10-RVA-K100	L	49.7 ± 3.9	14 ± 1
Alternative Scenarios: Reduced Space with Informed Management			
(U) O-R10-RVA-K150-IM		54.3 ± 3.7	18 ± 1
(V) C-R10-RVA-K150-IM		49.4 ± 3.9	20 ± 2

Underlined portions of the scenario name indicate where the scenario differs from the baseline scenario.

(E) = 14.5 % and 0.4 %, respectively. Relative projections for N_{100} did not differ between the eight PVA scenarios evaluated with and without incorporation of the results of the RVA (Figure 2A). Similarly, the average values of N were not significantly different with and without incorporation of the results of the RVA (151.75 vs. 138.75, respectively, $P = 0.1577$). Projected GD_{100} and F_{100} were more variable among the original PVA scenarios without incorporation of the RVA results (B1 = 0.65 and 0.68, respectively, H0: $\beta 1 = 1$, $P < 0.05$, Figure 2b and c). These overall results appear to be heavily influenced by the difference between one set of complementary scenarios, F and P. Scenario F had a lower $p(B) = 25\%$ compared to a $p(B) = 54.9$ % for scenario P. The much higher rate of breeding success due to the RVA function in scenario P results in an average N of 178 (compared to 115 in scenario F) and zero p(E) (compared to 14.5% p(E) in scenario F). The smaller population sizes in scenario F lead to greater inbreeding accumulation and a decrease in genetic diversity over time. Similarly, overall GD_{100} was significantly higher (0.9231 vs. 0.8927, respectively, $P = 0.0444$) and F_{100} was lower (0.0808 vs. 0.1086, respectively, $P = 0.0509$) across RVA-based scenarios due to the same trend in $p(B)_{avg}$ for these scenarios.

The effect of uncertainty on population projections

The percent of total variation in PVA projections explained by each of the factors included in the function determining a pair's probability of reproductive success on each genetic and demographic outcome after 100 years by population type are presented in Table 5. As expected, the outputs that were most affected by including the RVA results into the PVA models were the number of pairs that are needed to breed to the target population size (pairs) and the average proportion of pairs that were reproductively successful per year ($p(B)_{avg}$). The uncertainty in the positive effect of the female (or the pair) having prior reproductive success and the negative effect of female age on reproductive success explained the largest proportions of the variation in pairs and $p(B)_{avg}$, regardless of population type. Greater positive effects of both female parity and pair parity resulted in fewer pairs being needed each year and more pairs being reproductively successful per year, on average. The only factor that did not explain a statistically significant amount of variation in pairs and $p(B)_{avg}$ was a negative effect of the age difference between the male and female.

The uncertainty in the negative effect of female age on reproductive success had the greatest effect on the projections for GD_{100} and F_{100}. Greater negative effects of both male and female age resulted in lower GD in both population types and higher F in closed populations only. Greater positive effects of female parity resulted in higher GD in both population types, but F was unaffected.

Generally, there was a relatively small (Table 5), yet positive, impact of informed management within both open and closed populations. An informed management strategy resulted in lower F_{100}, fewer pairs needing to be made each year, and greater $p(B)_{avg}$ within open populations (Figure 3). Similarly, using an informed management strategy resulted in greater GD_{100}, fewer pairs needing to be made each year, and a greater $p(B)_{avg}$ within closed populations (Figure 4).

Discussion

Most PVA models for cooperative breeding programs in North America have been run using the program ZooRisk (Che-Castaldo *et al.*, 2019). Although the Vortex software program was initially designed for the simulation of in situ populations, our analysis contributes to growing examples that Vortex can also be utilized effectively for PVAs of ex

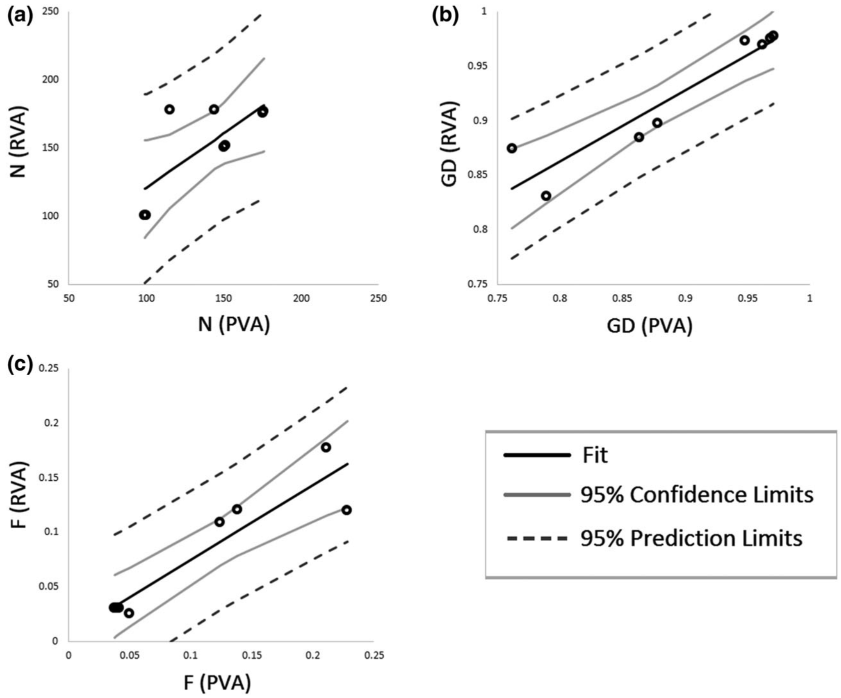

Figure 2 Relative average population projections for (a) population size, N, in year 100, (b) genetic diversity, GD, in year 100, and (c) inbreeding accumulation, F, in year 100, for 8 PVA scenarios of the North American ex situ fennec fox population evaluated in Vortex with and without incorporation of the results from the RVA.

situ populations, as the relative and average genetic and demographic predictions were generally the same across both software programs when given similar inputs. Consistent with prior knowledge of captive breeding programs, projections from both ZooRisk and Vortex suggest that lowering the probability of breeding success or shortening female reproductive lifespan results in smaller mean population size (i.e. below target size), more rapid genetic loss, and increased extinction risk. Also, open populations performed better than closed populations in both software programs.

Using Vortex for our PVA models allowed us to increase the complexity of our models to give each individual female (or pair) a unique probability of reproductive success based on a complex function dependent on the characteristics of the individual females and pairs that varied across iterations due to uncertainty in the effects of each factor on

Table 5 Percent of total variation in projection of genetic diversity (GD_{100}), inbreeding accumulation (F_{100}), number of pairs needed per year to breed to the target population size of 150 (average across years; Pairs), and average proportion of females that produce a litter per year ($p(B)_{avg}$) explained by management strategy (traditional vs. informed) and each of the factors included in the function determining a breeding pair's probability of reproductive success by population type (open vs. closed)

	GD_{100}		F_{100}		Pairs		$p(B)_{avg}$	
Factor	Open	Closed	Open	Closed	Open	Closed	Open	Closed
Management Strategy	0.12%	**0.15%**	**0.76%**	0.02%	**0.19%**	**0.09%**	**0.18%**	**0.08%**
Female Age (−)	**11.87%**	**52.04%**	0.04%	**0.98%**	**14.72%**	**29.65%**	**7.70%**	**29.91%**
Male Age (−)	**1.36%**	**7.65%**	0.01%	**0.25%**	**0.91%**	**3.58%**	**0.35%**	**4.01%**
Pair Parity: Yes/Yes (+)	0.01%	**1.87%**	0.00%	0.18%	**23.16%**	**17.03%**	**29.15%**	**18.02%**
Female Parity: Yes (+)	**1.24%**	**7.22%**	0.00%	0.09%	**32.98%**	**29.00%**	**35.96%**	**30.02%**
Age Difference (−)	0.00%	0.00%	0.22%	0.03%	0.00%	0.02%	0.00%	0.01%
Experienced Pair (+)	0.04%	0.00%	0.00%	0.01%	**0.14%**	**0.08%**	**0.11%**	**0.11%**
Pair Rearing Type: HR (+)	0.02%	**0.11%**	0.00%	0.00%	**0.27%**	**0.03%**	**0.35%**	**0.03%**
Pair Rearing Type: M (−)	0.12%	**1.50%**	0.01%	0.00%	**7.54%**	**5.50%**	**7.06%**	**4.38%**

Bold values indicate statistically significant factors.
(−), negative coefficient; (+), positive coefficient; HR, Hand reared; M, Mixed.

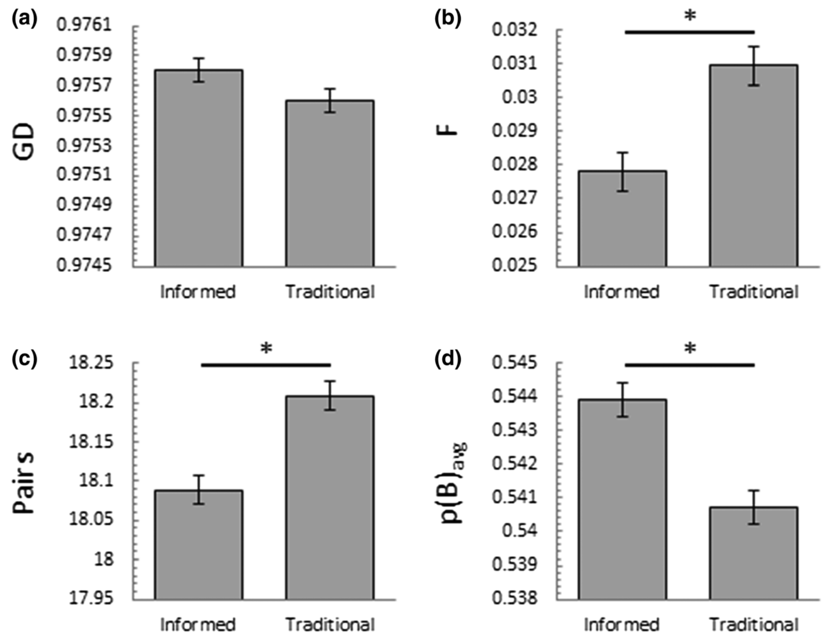

Figure 3 Population projections for (a) genetic diversity (GD) in year 100, (b) inbreeding accumulation (F) in year 100, (c) average number of pairs that were needed to breed to the target population size (Pairs), and (d) average proportion of females that were reproductively successful per year ($p(B)_{avg}$) across PVA scenarios for open populations, with or without an informed management strategy. Averages across 1000 iterations ± SE are presented. Horizontal bars with an asterisk (*) indicate a significant difference between management strategies ($P < 0.05$).

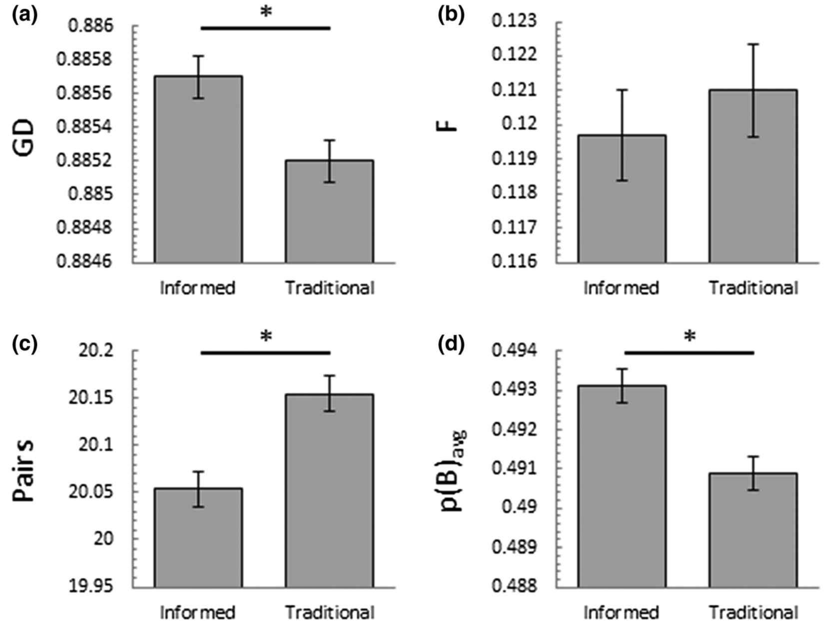

Figure 4 Population projections for (a) genetic diversity (GD) in year 100, (b) inbreeding accumulation (F) in year 100, (c) average number of pairs that were needed to breed to the target population size (Pairs) and (d) average proportion of females that were reproductively successful per year ($p(B)_{avg}$) across PVA scenarios for closed populations, with or without an informed management strategy. Averages across 1000 iterations ± SE are presented. Horizontal bars with an asterisk (*) indicate a significant difference between management strategies ($P < 0.05$).

reproductive success in the North American ex situ fennec fox population. Including a complex function for determining the probability of a female not producing a litter resulted in projections with lower probabilities of extinction, lower accumulation of inbreeding and a slower loss of genetic variation. The average rate of reproductive success among pairs in these RVA-based fennec fox PVA models was higher than the actual rate that has been observed in the current population (Bauman *et al*., 2019). This is likely the result of Vortex creating pairs that are more favorable than those that have been made historically by the program manager (e.g. females getting their first breeding opportunity at an earlier age). Logistical challenges such as lack of space for holding offspring, exhibit renovations, short-term health issues, financial constraints, and staffing changes, as well as permitting or regulatory issues may hamper shipments of animals, resulting in animals that are older when put together for breeding than originally planned. A highly skewed sex ratio in a population could also result in potential breeders waiting, and aging, until suitable mates become available. Additionally, Vortex is better able to estimate the probability of success for each pair, meaning that if there are genetically valuable animals with low success rates, Vortex will create more breeding pairs, many of which may have higher success rates, therefore raising the mean success rate across all recommendations. In practice, sometimes animal program managers may overestimate the probability of success of genetically valuable 'long shot' pairs, and in an effort not to overshoot capacity, may make fewer total breeding recommendations leading to an overall lower success rate. The consequences of this phenomenon are more optimistic population projections from our PVA models than may occur in reality. Taking this into consideration, we suggest that the most appropriate use of PVA for ex situ programs may be to compare the relative effects of different management strategies on population sustainability (Beissinger & Westphal, 1998; Reed *et al*., 2002), as opposed to predicting the actual values, unless model structure and inputs are constructed to better reflect real-world limitations (e.g. logistic constraints) and current management practices. Our results also suggest that changes should be made to the management of the fennec fox SSP to increase the overall average success rate across breeding pairs for the population to become more sustainable.

Although the management decision to bring in imports and allow exports (open vs. closed population type) had the greatest impact on genetic and demographic predictions for the ex situ fennec fox population overall, it cannot be ignored that the uncertainty in the effects of female age, male age, and female parity on reproductive success also resulted in significant variation in resulting genetic projections. Adaptive management decisions should improve our knowledge of these factors, thus, increasing the precision of these parameter estimates over time (Canessa *et al*., 2016). In order to do this, these particular attributes of individual animals should be considered more carefully when making breeding recommendations in this population. Increasing the accuracy for determining how many breeding pairs are needed to achieve the target lambda for a given breeding and transfer plan period will result in a wiser use of institutional resources, which when multiplied across species in the collections of multiple zoos, could be a significant saving of time, energy, financial investment, and space.

Sensitivity analysis revealed that having an informed management strategy can also improve genetic projections, regardless of population type. Although the effects may be small, when managing very restricted gene pools in very small populations with the hope that they persist for a long time, every little enhancement to the population helps. The beneficial effects of these adjustments will work in tandem with other adaptive management decisions based on the RVA results, to improve the status of this population. Thus, these strategies should be incorporated into the current management of the fennec fox SSP population to improve reproductive success among pairs and increase population sustainability over time.

Unfortunately, our current PVA models do not address some of the other factors affecting reproductive success and population sustainability. In 2015, the AZA Wildlife Contraception Center was renamed the AZA Reproductive Management Center (RMC) to reflect its expanded scope of tackling population-level threats to sustainability related to reproduction. Although the RMC still serves as the central clearinghouse for contraception data in the U.S., its research on infertility (Asa *et al*., 2014) has led to new initiatives such as Lifetime Reproductive Planning, an innovative approach to reproductive management in ex situ populations. Studies in a diverse range of taxa have demonstrated a link between infertility and delayed or infrequent breeding of females (Asa *et al*., 2014; Penfold *et al*., 2014). Lifetime Reproductive Planning proposes to plan a female's reproductive life from birth, rather than during each breeding and transfer plan period, by spacing breeding opportunities using contraception or separation. Reproductive strategies will be designed in such a way as to first establish fertility and then maintain it. However, the effect that these new reproductive strategies will have on populations is unknown.

Exploration of lifetime reproductive strategies via PVA models will not only allow the evaluation of the demographic and genetic impacts of various reproductive management scenarios on the population, but will also identify ideal breeding intervals for a given species in order to maximize reproductive lifespan while minimizing exposure to contraception and non-breeding estrous cycles, without producing excessive surplus offspring. This approach is especially needed for carnivores, since the time to reversal for the safest long-term contraceptive for that taxon, Suprelorin® (Virbac, Milperra, Australia), is not predictable (Larson *et al*., 2013; Fontaine, 2015; Putnam *et al*., 2015). Therefore, carnivore population managers face unique challenges and are in urgent need of additional tools for reproductive planning. The RMC's next step is the incorporation of Lifetime Reproductive Planning into PVA models using Vortex.

Our study demonstrates that Vortex is capable of projecting the viability of ex situ populations with flexibility, and has the ability to incorporate complexity and uncertainty into population parameters. Moving forward, Vortex's capacity for complexity will be a major asset and will be utilized to investigate the effects of different lifetime reproductive strategies for females on the demographic and genetic projections of ex situ populations, as it promises to be an innovative tool to inform ex situ population management and improve population sustainability. Additionally, this study revealed that making breeding recommendations that are informed by RVA will improve population sustainability. RVA should be done periodically to track and incorporate changes in the importance of different factors over time. Other managers of populations that are struggling with similar issues of inconsistent reproduction may find it beneficial to conduct similar analyses for their populations. The approach taken in this study to project population genetic and demographic outcomes as a result of explicit consideration of factors driving reproductive success is also applicable to managing free-ranging populations of animals. Traits examined in wild populations might be body condition, breeding experience, duration of pair bonds, dominance status and habitat quality, all of which might be affected by management practices and can be modeled in Vortex. The incorporation of individual and pair properties that drive reproductive success into PVA models would allow both improvement in the robustness of model predictions and the ability to examine management actions that affect those properties.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Model parameters used in baseline scenario for an open fennec fox SSP population (scenario A) of the PVA in ZooRisk and Vortex.