# Expected demographic and genetic declines not found in most zoo and aquarium populations

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Since the 1980s, animals in accredited zoos and aquariums have been managed as populations through cooperative breeding, with a goal of maintaining ex situ populations that are as demographically viable and genetically diverse as possible. Here, we provide what we believe to be the first large-scale assessment of whether cooperative breeding programs are achieving this goal over time. Using a comprehensive dataset spanning nearly 20 years and encompassing more than 400 ex situ vertebrate populations, we applied Bayesian hierarchical modeling to quantify changes in seven population metrics over time. Instead of the general declines expected for small and often closed populations like those in zoos and aquariums, we found no change in the demographic and genetic characteristics of the majority of these populations. Our results indicate that while some zoo and aquarium populations are currently unsustainable, cooperative management is helping to slow or prevent declines in the health of many ex situ populations.

Zoos and aquariums ("zoos" hereafter) are becoming broadly recognized as important partners in conservation (Conde *et al.* 2011; IUCN SSC 2014). Their wide-ranging contributions include providing animals for and supporting reintroductions (Gilbert *et al.* 2017), field-based monitoring and research (Che-Castaldo *et al.* 2018), and management of ex situ animal populations (Balmford *et al.* 1996; Conway 2011). Although not appropriate for all threatened species, ex situ management offers an additional recovery strategy alongside threat abatement and habitat protection (Redford *et al.* 2012; IUCN SSC 2014). To serve their conservation roles effectively, ex situ populations should be demographically and genetically stable (Lees and Wilcken 2009; Ballou *et al.* 2010). To this end, accredited zoos have coordinated the breeding and exchange of animals among facilities through cooperative breeding programs since the 1980s (Ballou *et al.* 2010; Ballou and Traylor-Holzer 2011).

However, recent research has raised questions about the ability of zoos to maintain viable ex situ populations in the long term (Lees and Wilcken 2009; Conway 2011), as well as the effectiveness of cooperative management programs overall (see Powell *et al.* 2019). A substantial number of zoo populations fail to meet demographic and genetic indicators of sustainable populations, in that the populations are very small or have low genetic diversity (Leus *et al.* 2011; Long *et al.* 2011; Che-Castaldo *et al.* 2019). These studies focused on "snapshots" of present status or future projections, but did not examine whether and how population status has changed historically.

Placing the current status of each population in the context of an earlier time point enables examination of whether populations have improved over time even though they may not be fully self-sustaining.

In the absence of management, small and closed populations like those in zoos are generally expected to decline in demographic and genetic health, becoming smaller and more inbred over time (Lacy 1997; Ballou *et al.* 2010). This expectation is for a directional change rather than a specific amount or rate of decline in most demographic and genetic metrics. However, for gene diversity, one null expectation is the loss of diversity due to genetic drift (Lacy 1995; Earnhardt *et al.* 2004). Aspects of active management, such as recruiting unrelated potential founders (those present still but without descendants, as well as those from outside sources), equalizing founder representation, and prioritizing breeding pairs to minimize inbreeding, can slow or even reverse these expected declines. The detailed records kept for zoo populations as part of cooperative management allow for quantification of these possible changes.

The Association of Zoos and Aquariums (AZA) and its member facilities, mainly in North America, manage more than 500 ex situ animal populations as Species Survival Plan® (SSP) Programs ("Programs" hereafter; Figure 1; Powell *et al.* 2019; AZA 2020). Taxon Advisory Groups (TAGs) oversee and support groups of Programs for similar taxa (eg felids, passerines). AZA scientific advisors assist Programs in developing management plans known as Breeding and Transfer Plans (BTPs) every ~1–3 years based on analyses of studbook data to quantify the population's genetic and demographic status. Advisors apply small population management theory and methods (Lacy 1995; Ballou *et al.* 2010) to determine recommended mating pairs and animal transfers needed to reach the Program's target size while minimizing the population's mean kinship, which has the effect of maximizing genetic diversity

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**Figure 1.** A flock of Chilean flamingos (*Phoenicopterus chilensis*) within the ex situ population managed as a Species Survival Plan (SSP) Program by the Association of Zoos and Aquariums (AZA).

and minimizing inbreeding and adaptation to captivity (Ballou *et al.* 2010). In 2008, the PMCTrack database (Faust *et al.* 2011) was built to compile BTP recommendations, their outcomes, and the demographic and genetic characteristics of each population summarized in BTPs (Faust *et al.* 2019).

We used PMCTrack to evaluate how the demographic and genetic status of managed vertebrate populations has changed over time, and relative to Program targets and goals. The earliest BTP recorded in PMCTrack for each population was set as the starting point for comparison, which is later than the start of management for most populations. We constructed Bayesian hierarchical models to estimate trends in demographic and genetic metrics for each Program. This approach incorporates uncertainty into trend estimates both within and across Programs, improving upon the current lack of consideration for uncertainty in ex situ population assessments (Lacy 2019). It also leverages all existing data through partial pooling, which results in conservative estimates that are less sensitive to noise in the dataset, and can improve estimates for Programs with sparse data (Gelman and Hill 2007). Our results provide insight into the effectiveness of cooperative management, by assessing whether zoo populations have declined or improved in demographic and genetic health during active management.

## Methods

We compiled data from BTPs in PMCTrack through December 2017, retaining only BTPs for populations currently managed as SSP Programs. We focused on bird, mammal, and reptile species due to small sample sizes for fish and amphibians (nine and seven Programs, respectively). From retained BTPs, we compiled data on demographic and genetic metrics (Table 1), target population sizes, and 14 biological and programmatic variables that could explain potential differences in Program metrics and their trends over time (see "Predictors" in Table 1 for a full list). Genetic metrics were calculated based on pedigree analyses of studbook data (see Lacy 1995; Ballou *et al.* 2010) rather than molecular analyses. In particular, gene diversity (GD) was estimated relative to that of a hypothetical founding population, in which all founders were presumed to be unrelated and maximally genetically diverse. Founder genome equivalents (FGE; Table 1) is a genetic metric used to describe ex situ populations, and represents the number of these hypothetical, unrelated individuals ("founders") that would be needed to produce the current level of GD.

### Summary of current status from the most recent BTPs

We summarized the current status of zoo populations by taxonomic group and AZA Program designation. We included only the most recent BTP for each of the Programs that were actively managed at the time of study (n = 434 Programs). Of these, 74 Programs had only one BTP, and therefore were excluded from the trends analysis (see below). The majority of these most recent BTPs (n = 410) were from 2014–2017, with the earliest from 2009. Genetic metrics were not calculated in BTPs for 29 Programs because they lacked sufficient pedigree information.

### Summary of historical population trends over time

We assessed trends in demographic and genetic metrics over time, focusing on the 371 Programs with at least two BTPs that also contained data on population size. This included eight Programs that were no longer actively managed and excluded from the current status summary (see above). This dataset mainly spanned the years 2000–2017 (one BTP was in 1999), with the average time between the first and last BTP for individual Programs being 8.5 years (WebFigure 1). We analyzed seven demographic and genetic metrics as response variables (Table 1), which were log- or logit-transformed where necessary (WebTable 1).

We constructed Bayesian hierarchical models to quantify the change in metrics over time using all available BTPs for each Program (WebPanel 1; WebTable 1). Briefly, we modeled the predicted metric value from each BTP as a function of

**Table 1. Summary of demographic, genetic, and predictor metrics compiled from Breeding and Transfer Plans (BTPs) for animal populations managed as Association of Zoos and Aquariums (AZA) Species Survival Plan (SSP) Programs**

| Type | Metric (abbreviation) | Description |
| --- | --- | --- |
| Demographic | Population size ($n$) | Number of currently living individuals in the population |
| | Growth rate (lambda) | Finite rate of population growth calculated as the geometric mean of changes in total population size over the past 5 years ("5-year lambda" from BTPs) |
| | Distance from target size | Absolute difference between current population size and target population size, determined by the Taxon Advisory Group's most recent Regional Collections Plan and/or discussions between AZA advisors and Program Leaders |
| Genetic | Gene diversity (GD) | Current percentage of founding gene diversity retained; cooperative management aims to maximize GD in the managed population |
| | Inbreeding level ($F$) | Mean inbreeding level; cooperative management aims to minimize $F$ in the managed population |
| | Founders | Number of founders represented in the current population; a founder is an individual from a source population (often the wild) that has reproduced and has no known relationship to any individuals in the managed population except for its own descendants |
| | Founder genome equivalents (FGE) | Current founder genome equivalents, a metric developed for measuring genetic variation in ex situ populations (Lacy 1995); it is expressed in units of the number of wild-caught, unrelated individuals ("founders") that would produce the same gene diversity as the current population |
| Predictors | Taxon | Taxonomic class: Reptilia, Mammalia, or Aves |
| | Program type | AZA Program designations: Green, Yellow, or Red SSP Programs; designation is based on population size, projected gene diversity, and other factors (see AZA 2020), with Green being most viable |
| | Program scope | Regional or international |
| | Program age | Time between program start date and January 1, 2018, in years |
| | Plan age | Age of most recent BTP based on time between finalization date and January 1, 2018, in years |
| | Knownness | Percent pedigree knownness after pedigree assumptions and animal exclusions are applied |
| | Facilities | Number of facilities involved in most recent BTP |
| | Body size | Median body size, in kilograms |
| | Generation time | Mean generation time, in years |
| | Generations observed | The number of years observed between the first and last BTP divided by the species' mean generation time |
| | Litter size | Mean litter or clutch size |
| | Age at first reproduction | Age at first reproduction for females, in years |
| | Median life expectancy | Expected lifespan, in years, based on pooled data across male and female individuals from studbook data |
| | Reproductive lifespan | Length of age range in which females are reproductive, in years |
| | IUCN category | IUCN Red List category, summarized into "Data Deficient", "Lower Risk" (NT, LC), and "Threatened" (CR, EN, EW, or VU) |

time, estimating the intercept and slope for the relationship between metric and time for each Program. For each metric, we tested whether the inclusion of (1) separate variance estimates among BTPs for each Program or (2) separate slope estimates for each TAG were necessary, or if a simpler model without those terms would yield similar results. The estimated slopes measured the annual rate of change (or "trends") in each metric for each Program. We used the 95% credible interval for each slope estimate and the appropriate reference value for each metric (WebTable 1) to determine whether a Program metric increased (eg the interval was greater than the reference value), decreased (eg the interval was smaller than the reference value), or did not change (eg the interval encompassed the reference value) over time. To explore the importance of dataset length, we repeated the same calculations using only Programs for which the observed period covered at least the average length of time spanned by two generations for each species ($n = 42$).

For GD, we additionally compared the estimated slopes against the rate of loss expected under the null hypothesis of genetic drift. In the absence of mutation, immigration, and natural selection, and with statistically truly random mating, a population's GD after $t$ generations is expected to decline due to genetic drift, calculated as (Lacy 1995; Earnhardt *et al.* 2004):

$$GD_t = \left(1 - \frac{1}{2N_e}\right)^t GD_0 \qquad \text{Equation 1}$$

where $GD_0$ is the starting GD from the first BTP and $N_e$ is the starting effective population size (calculated in BTPs of 297 Programs). To derive an odds ratio with a one-unit increase ($GD_1/GD_0$) that is comparable to the slopes estimated from our model, we calculated the annual change expected ($[GD_t - GD_0]$/the number of years observed) and added it to $GD_0$ to obtain $GD_1$. We then tallied whether the credible interval for
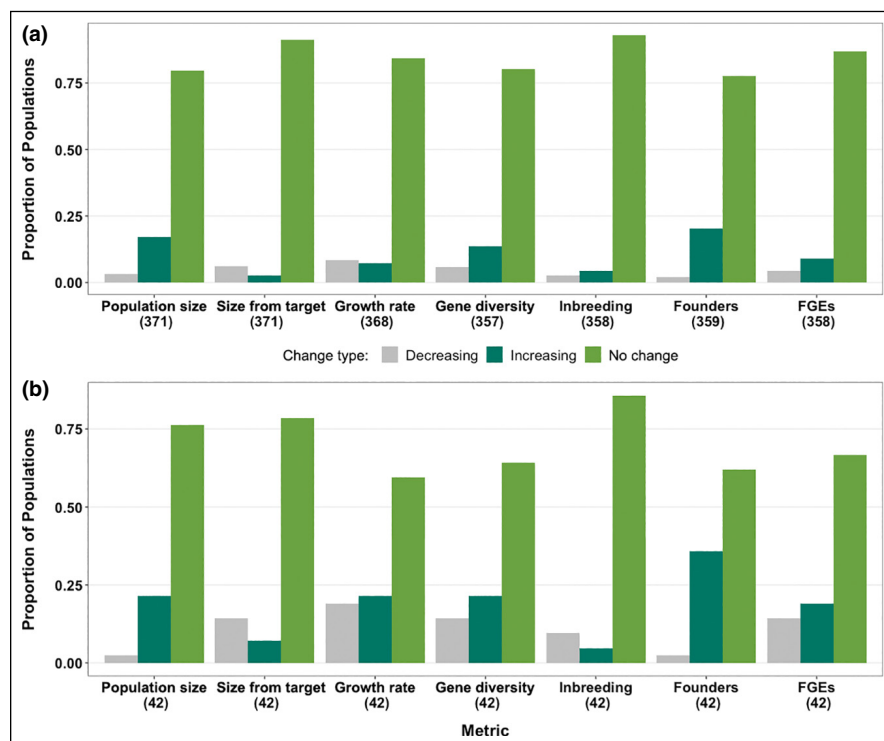
**Figure 2.** Summary of demographic and genetic trends over time (2000–2017) in AZA animal populations for (a) all populations studied and (b) only those with data that spanned at least two generations. Estimated slopes from fitting each metric as a function of time are grouped into whether they indicate a decreasing, increasing, or no change trend over time. Number of Programs with data for each metric are indicated in parentheses. FGE = founder genome equivalents.

each slope estimate was greater than, less than, or encompassed the expected slope value for the Program (indicating less decline than, more decline than, or declined as expected under the null, respectively).

### Patterns in historical population trends over time

We further analyzed the slope estimates to examine whether there were patterns in how Programs changed over time, using predictor variables in Table 1. We used classification and regression tree methods called conditional inference tree (*ctree*) and conditional random forest (*crf*) from the R package *party* (Hothorn *et al.* 2006) to identify the most important predictors of slope estimates for the seven metrics. We set the analysis parameters to 1000 trees, four variables tried at each node (*mtry* = 4), and default values for all other parameters. We implemented all statistical analyses using R (v3.6.2; R Core Team 2019); all code, data, and trend results for each Program are archived on Figshare (https://dx.doi.org/10.6084/m9.figshare.11845518).

### ■ Results

### Summary of current status

Demographically, zoo populations averaged 116 individuals in size with high variation (standard deviation [SD] = 162

individuals; WebTable 2). Only ~13% of Programs had ≥200 individuals, a proposed indicator of population viability (Lees and Wilcken 2009). Programs were on average growing slightly (lambda = 1.03 ± 0.08 SD), and 66% of Programs had stable or increasing population growth rates over the past 5 years (WebTable 2).

Genetically, zoo populations retained on average 90% (± 8% SD) of their founding GD, with higher average GD for birds and reptiles than mammals (WebTable 3). Average inbreeding (*F*) was 0.05 (± 0.08 SD), just below the expected kinship of offspring from mating between first cousins (*F* = 0.0625; Lacy 1995). On average, populations were descended from 27 (± 28 SD) founders, and had gene diversity equivalent to that of nine (± 11 SD) unrelated individuals (based on the FGE metric). Nearly half of Programs were descended from ≥20 founders, and 12% from ≥50 founders (20–50 founders have been recommended for ex situ populations whose primary role is long-term insurance against extinction; Lees and Wilcken 2009). Although FGE is not expected to equal the actual number of founders, we examined how many populations had 20–50 FGEs, as no recommendations presently exist for this metric. Only 8% and 1% of Programs had gene diversities equivalent to that of 20 founders and 50 founders, respectively.

### Summary of historical population trends over time

Based on slope estimates from the Bayesian models, the majority of the 371 Programs with longitudinal data did not change in demographic and genetic metrics over time (77–93% of Programs, depending on the metric; Figure 2a). For Programs that did change over time, a greater proportion increased in population size, GD, number of founders, FGEs, or inbreeding level, or moved closer to their target size over time, compared to the proportion with the opposite trends (Figure 2a). Similar proportions of Programs increased and decreased in population growth rates over time.

Comparable patterns were observed when only the 42 Programs with data spanning at least two generations were considered (Figure 2b). The majority (60–86%) of these Programs showed stable trends across metrics, and the remaining Programs were distributed into decreasing and increasing trends in proportions similar to when all Programs were examined (Figure 2a). Two notable differences included a larger proportion of Programs that increased in number of founders, and more Programs had declining than increasing inbreeding levels.

Most Programs (80%) exhibited changes in GD consistent with that expected under genetic drift (Figure 3a). Moreover,

48 Programs (16%) had declines in GD that were even smaller than expected under drift, which was four times the number with declines greater than expected (12 Programs, or 4%). Of those 48 Programs, 39 had increasing trends in GD, which is not expected under genetic drift. When considering only the Programs with data that spanned at least two generations (Figure 3b), an even larger proportion of Programs declined less than expected (28%), but a larger proportion declined more than expected as well (10%). When only the point values were examined (ie without incorporating uncertainty via modeling), the actual GD reported in the most recent BTP was higher than the expected GD under genetic drift ($GD_t$) for every Program.
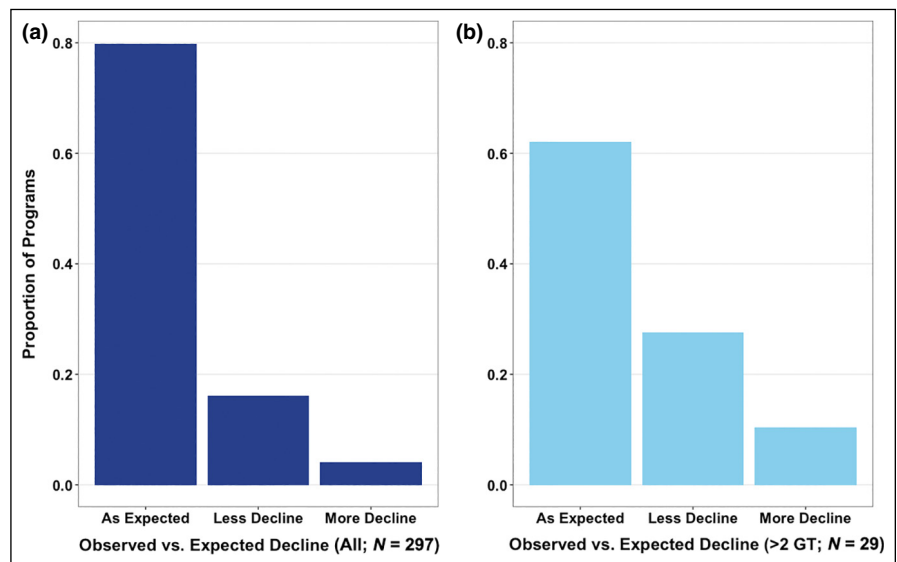


**Figure 3.** Comparison of the observed change in gene diversity (GD) against the expected change under a null hypothesis of genetic drift, for (a) all populations studied and (b) only those with data that spanned at least two generations (GT = generation time).

## Patterns in historical population trends over time

A subset of Programs with data on all 15 predictor variables were included in the conditional random forest analyses (202–205 Programs, depending on the metric; WebTable 4). Models for trends in population size and distance from target size had the highest explanatory power (>30%; WebTable 4). For trends in distance from target size, both the *ctree* and *crf* models identified "taxon" and "IUCN category" as important predictors (IUCN = International Union for Conservation of Nature). Compared to Programs for bird species, those for mammals and reptiles moved closer to target size over time, especially those in more threatened IUCN categories (ie Critically Endangered [CR], Endangered [EN], Extinct in the Wild [EW], and Vulnerable [VU] compared to Not Threatened [NT] and Least Concern [LC]; Figure 4). For trends in population size, both the *ctree* and *crf* models identified "program type" as an important predictor. Programs with Green and Yellow designations tended to increase in population size, whereas those with Red designations tended to decrease (WebFigure 2); these AZA Program designations are based on population health (including size), Program goals, and other factors, and reflect different management schemes (Table 1; AZA 2020). The *crf* model also indicated "generation time" was an important predictor, with shorter generation times correlated with greater increases in population size (WebFigure 3). We did not find patterns in how population growth rates changed over time.

For trends in genetic metrics, the models had slightly lower explanatory power (24–28% variance explained; WebTable 4). The *ctree* and *crf* models consistently identified "taxon" as an important predictor of all genetic metrics except inbreeding. Based on the *ctree* models (not shown) for the remaining four metrics, bird and mammal Programs had stable genetic metrics, whereas reptile Programs increased in GD, founders, and FGEs over time (WebFigure 4). We did not find patterns in how inbreeding levels changed over time.

## ■ Conclusions

Our study adds to previous research demonstrating that most zoo populations currently fail to meet proposed indicators of long-term sustainability (Lees and Wilcken 2009; Leus *et al*. 2011; Long *et al*. 2011). Specifically, ~87% of populations examined had fewer than 200 individuals, and 51% were descended from fewer than 20 founders. However, our study is the first to provide evidence that cooperative management is helping to prevent the demographic and genetic declines that would be expected in the absence of management. Small populations are more susceptible to demographic stochasticity, genetic drift, and the effects of inbreeding depression, and therefore zoo populations are expected to decrease in size and genetic variation over time (Lacy 1997; Ballou *et al*. 2010). In contrast to these directional expectations, we found that the majority of zoo populations have maintained stable demographic and genetic metrics over time. Moreover, most populations did not decline in GD more than expected under the null hypothesis of genetic drift, and a sizeable proportion declined less than expected or even increased in GD.

Thus, while concerns about the current status of zoo populations are justified, our finding of mostly stable trends suggests cooperative management is having an impact by slowing or preventing the expected general declines. Given the severity of the biodiversity crisis, prevention of further declines is a common conservation goal (eg Convention on Biological Diversity Aichi Biodiversity Target 5, www.cbd.int/sp/targets), and therefore stability can be considered an achievement in
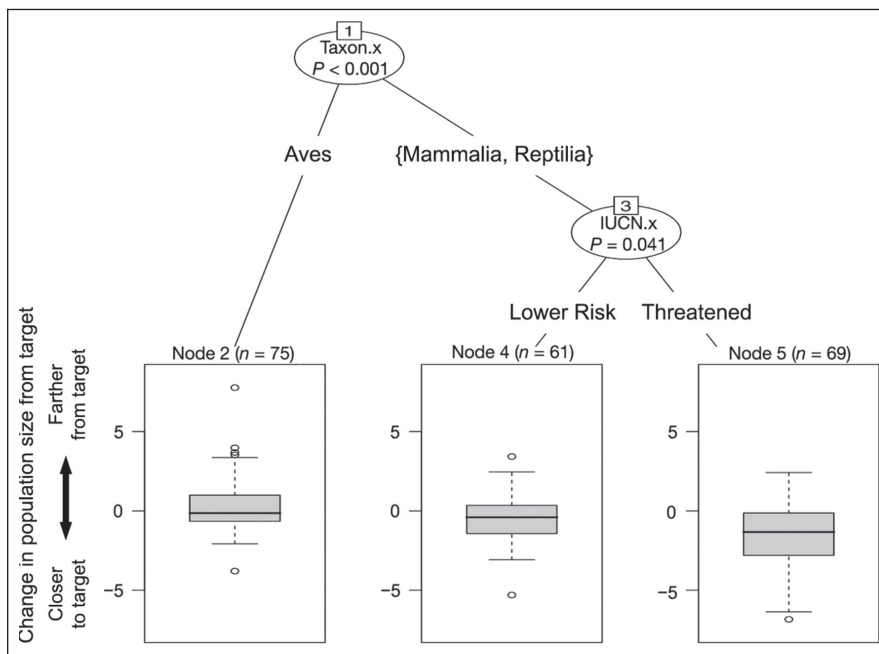
**Figure 4.** Conditional inference tree (*ctree*) showing the important predictors (Taxon, IUCN category) of the trend in distance from target size over time. The boxplots show the estimated slopes (unit = number of individuals changed per year) from fitting the metric (absolute difference between population size and target size) as a function of time, with a value of zero indicating no change, larger than zero is an increasing difference (or getting farther from target size), and smaller than zero is a decreasing difference (or getting closer to target size) over time. In the boxplots, thick lines represent medians; box bottoms and tops represent the 25th and 75th quartiles, respectively; lower edges of whiskers represent the 25th quartile minus 1.5 times the interquartile range (IQR) or the minimum slope value, whichever was greater; upper edges of whiskers represent the 75th quartile plus 1.5 times the IQR or the maximum slope value, whichever was smaller; open circles represent slope values that fall outside the range of the whiskers. The number of Programs in each subset or node is indicated in parentheses.

itself. Furthermore, of the populations with changing genetic trends, a larger proportion increased in GD, founders, and FGEs than those with opposite trends. Similar to Earnhardt *et al.* (2004), we found that managed populations generally had higher GD than the point estimates predicted under genetic drift, and that a number of populations increased in GD over time, which cannot be predicted by drift. These results indicate that cooperative management may not only maintain but also improve the genetic health of zoo populations. Trends in inbreeding levels were more mixed, with levels increasing in slightly more populations than decreasing over time, but this was reversed when we focused on populations with at least two generations observed. In closed populations, genetic metrics can improve as potential founders begin to reproduce, or as family lines become more equally represented in the population. Without additional founders, GD is expected to eventually decline, but for longer-lived species the increasing trend may last for years.

Of the populations with changing demographic trends, more populations increased in size than decreased. However, this increase cannot automatically be equated with improvement, as population growth may not be a goal for every Program; indeed, maintaining or even lowering population size for various reasons (eg lack of space) may be specific objectives of some Programs. More populations grew closer to their target sizes than away from them, which may be more clearly considered an improvement. Still, there are limitations to interpreting this metric, because target sizes are not determined systematically across Programs (Earnhardt *et al.* 2001) and may still be too small to ensure long-term population viability. Furthermore, target sizes can change over time as managers revise them during the development of Regional Collection Plans (AZA 2020). Additional research is needed to distinguish whether populations are trending closer to their original target sizes, or whether targets are being adjusted to match observed population trends.

Trends in demographic and genetic metrics differed primarily based on taxonomic grouping. We found that mammal and reptile populations, and especially threatened species in those taxa, trended closer to target sizes over time than did bird populations (Figure 4). Possible explanations include mammal and reptile Programs being more carefully managed to reach target sizes, and/or managers setting more accurate or realistic targets that can be reached within the management timeframe. In terms of genetic metrics, birds and mammals exhibited stable trends, whereas reptiles displayed improving trends. Reptile populations tend to have more frequent or a larger number of animal importations (eg from other zoo regions, wild populations, or illegal trade confiscations), which could improve genetic metrics over time. Reptile Programs may also be newer, with potential founders just starting to breed, although Program age was not an important predictor in our analyses.

A valid concern is whether our dataset encompassed sufficiently long observation times to enable detection of unstable demographic and genetic trends, as Programs differed in the length of time represented by their BTPs. On average, Programs had 8.5 years of data between their first and last BTP (WebFigure 1), which may or may not have been adequate for populations to substantially change in demographic or genetic metrics, depending on the species' life history. However, when we accounted for generation times relative to observation periods, the patterns remained largely the same or better (Figures 2b and 3b). We chose the threshold of two generations based on data availability (only nine Programs had at least three generations observed), but two generations can be a sufficient time span to detect change if it occurs (eg Palm *et al.* 2003; Moraes *et al.* 2017). Moreover, the number of generations covered in the observation period was not an influential predictor for any metric, meaning

Programs with more generations observed were not more likely to experience change. We did find that species with shorter generation times had larger increases in population size (WebFigure 3), but we could not distinguish whether this was because increases for longer-lived species were not yet detectable, or because species with "faster" life histories had higher reproductive rates in ex situ settings and therefore could increase in population size. Nevertheless, we recognize that our dataset may still encompass too brief a time span for changes to be detected, and consequently these analyses will need to be updated as longer datasets are accrued. It is also possible that some Programs have changed considerably since their cooperative management began but that change occurred before data collection began in 2000. Program age was not an important predictor of trends, however, suggesting that trends were similar in older and newer Programs.

To fully evaluate management effectiveness, we would ideally compare observed population trends against expectations for each Program. The available data allowed us to use Program-specific target sizes and expectations under genetic drift as benchmarking points. In both cases, more Programs had positive than negative trends or outcomes, while the majority of Programs were stable or as expected. However, some Programs may aim to maintain rather than improve these metrics, and still others may aim to decline in metrics if that is what is most feasible or appropriate for the species. If Programs provided consistent and clear descriptions of the intended primary roles for their ex situ populations (eg reintroduction, insurance, research, or education; AZA 2020), as well as quantitative goals (eg stability, or some amount of growth within a timeframe), it would be possible to narrow the set of populations for analysis and evaluate population trends relative to those goals. Finally, additional data on grouping factors (other than TAGs) or Program-level characteristics (eg species life-history traits) could be incorporated into the hierarchical model to improve trend estimates.

We present here the first analysis of how demographic and genetic metrics of viability have changed in ex situ animal populations over time, using PMCTrack data on AZA Programs. Although the results of this study provide a more positive outlook on zoo population management than previous studies, it must be emphasized that analysis of the most recent BTP data indicates that a large proportion of zoo populations are currently not sustainable in the long term. Although not all species with managed populations in zoos are threatened (Che-Castaldo *et al*. 2018) and not all threatened species are appropriate for ex situ breeding (Conde *et al*. 2011; IUCN SSC 2014), maintaining viable animal populations continues to be an important way in which zoos and aquariums help to preserve biodiversity (Balmford *et al*. 1996; Conway 2011). Continually assessing the effectiveness of cooperative management programs is therefore key to improving the ability of zoos and aquariums to serve as partners in conservation.

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## Supporting Information

# FrontiersEcoPics

### On the lookout for the endangered, only to find the invasive

Among the most worrisome threats to Mediterranean Sea habitats are the range expansions of invasive species and declines of native species. An ongoing (disease-related) mass mortality event has brought the native Mediterranean fan mussel (*Pinna nobilis*) to the brink of extinction. Using nylon-mesh collectors, we assessed larval *P nobilis* recruitment at selected sites in the Columbretes and Balearic islands, in the northwest Mediterranean. Before the mortality event, which had begun in 2016, *P nobilis* juveniles were very common in our samples; in 2020, however, not a single juvenile was collected. Recently, and to our surprise, another bivalve species appeared in our samples: the pearl oyster (*Pinctada imbricata radiata*), a Lessepsian invader (that is, from the Red Sea via the Suez Canal) that was first reported (as adults) on the mainland coast of Spain in 2019. However, the larval recruits of this invasive oyster were detected in our collectors in the Balearic Islands almost one year earlier in 2018.

Although *P imbricata radiata* adults have yet to be recorded in the Columbretes Islands, which are located between the Spanish mainland and the Balearic Islands, this small 1-cm-long juvenile (pictured) was collected there in 2020. Our findings highlight adverse environmental outcomes from the perspective of larval dispersal. Larval collectors can serve as a means to document the recovery (or in this case, the loss) of native species and at the same time provide an early alert for invasions. Is the establishment of the nonnative *P imbricata radiata* and the extinction of the imperiled native *P nobilis* imminent? While the first outcome might be unavoidable, we can only hope to find fan mussel juveniles in our collectors again soon.

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