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RESEARCH ARTICLE

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Flock size and structure influence reproductive success in four species of flamingo in 540 captive populations worldwide

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Abstract

As global wildlife populations continue to decline, the health and sustainability of ex situ populations in zoos and aquariums have become increasingly important. However, the majority of managed ex situ populations are not meeting sustainability criteria and are not viable in the long term. Historically, ex situ flamingo (*Phoenicopteriformes*) populations have shown low rates of reproductive success and improvements are needed for long-term viability. Both flock size and environmental suitability have previously been shown to be important determinants of ex situ flamingo reproductive success in a limited number of sites in some species. Here we combined current and historic globally shared zoological records for four of the six extant species of flamingo (*Phoeniconaias minor*, *Phoenicopterus chilensis*, *Phoenicopterus roseus*, and *Phoenicopterus ruber*) to analyze how flock size, structure, and climatic variables have influenced reproductive success in ex situ flamingo populations at 540 zoological institutions from 1990 to 2019. Flock size had a strong nonlinear relationship with reproductive success for all species, with flock sizes of 41–100 birds necessary to achieve ca. 50% probability of reproduction. Additionally, an even sex ratio and the introduction of new individuals to a flock both increased ex situ reproductive success in some cases, while climatic variables played a limited role. We demonstrate the conservation management potential from globally shared zoological data and provide species-specific management recommendations to increase the reproductive success of global ex situ flamingo populations: minimum flock sizes should be increased, and we encourage greater collaboration between individual institutions and regional associations in exchanging birds between flocks.

KEYWORDS

conservation, data, management, population, sustainability

1 | INTRODUCTION

Wildlife populations are declining worldwide resulting in heightened extinction risks (WWF, 2020). As a result, the conservation of remaining populations is seen as a priority, and the ex situ management of populations in zoological collections has shown some success in preventing species extinctions (Bolam et al., 2021). Collectively, the global zoo and aquarium community manages 15% of all threatened terrestrial vertebrates in institutions which are part of internationally recognized organizations, such as the European Association of Zoos and Aquaria (EAZA) and the Association of Zoos and Aquariums (AZA) (Conde et al., 2011). The effectiveness of ex situ conservation relies on the ability of zoos and aquariums to maintain genetically and demographically sustainable populations. However, the sustainability of ex situ populations is hindered by small population sizes, low genetic diversity, limited reproductive success, and limited species holding capacity (Che-Castaldo et al., 2019). As a result, the majority of co-operatively managed ex situ populations are not meeting sustainability criteria and will not persist in the long term unless changes are made to collection planning and population management (Lees & Wilcken, 2009).

Flamingos (*Phoenicopteridae*) have been kept in captivity since the Roman period and are one of the most commonly represented avian taxa in zoological collections (Ogilvie & Ogilvie, 1986; Rose et al., 2014). Although ex situ populations exist for all six extant flamingo species, the greater flamingo (*Phoenicopterus roseus*), Chilean flamingo (*Phoenicopterus chilensis*), and American flamingo (*Phoenicopterus ruber*) are the most widely represented species (93% of all EAZA flamingos), followed by the lesser Flamingo (*Phoeniconaias minor*; 6%). The Andean flamingo (*Phoenicoparrus andinus*) and puna flamingo (*Phoenicoparrus jamesi*) have negligible ex situ populations and are considered low priority for future ex situ management (King & Bračko, 2014). In the wild, flamingos are increasingly threatened by habitat loss and pollution, with IUCN Red List status ranging from Least Concern (*P. roseus* and *P. ruber*) to Near Threatened (*P. minor*, *P. chilensis*, and *P. jamesi*) and Vulnerable (*P. andinus*) (IUCN, 2022). Despite the popularity of flamingo exhibits and their prevalence, zoos are unable to maintain self-sustaining ex situ populations for any flamingo species in all regions, with all species having historically relied on the importation of wild-caught individuals (Brown & King, 2005; Shannon, 2000). This has been primarily due to poor reproductive success and high egg loss, particularly in *P. minor*, *P. andinus*, and *P. jamesi* (Brown & King, 2005; King, 1994; Pickering, 1992).

Although some institutional flamingo flocks breed well, often in very large flocks, an overall deficit in the number of captive flamingos still exists (King & Bračko, 2014; Rose *pers. obs.*). Poor reproductive success, combined with increasing difficulties in sourcing wild-caught individuals, means that the sustainability of ex situ flamingo populations has become a concern among population managers (Brown & King, 2005; King, 1994; Rose et al., 2014). Improved management practices and increased knowledge surrounding the basic reproductive biology of all flamingo species are necessary if populations are to become self-sustaining in all regions (King, 1994; Rose et al., 2014).

Multiple factors are important in determining reproductive success in captive flamingos, ranging from flock composition (including flock size, sex ratio, and age structure) and management, to enclosure design, diet, and environmental suitability (Pickering et al., 1992). A clear positive relationship exists between flock size and reproductive success in captive flamingos (King, 2008; Pickering et al., 1992; Sandri et al., 2018; Stevens & Pickett, 1994). Larger flocks reproduce more frequently and also rear a greater number of chicks compared to smaller nonreproductive flocks (Pickering et al., 1992). Although flamingos can reproduce in very small flocks given suitable conditions, consistent reproduction only appears to be achieved above minimum flock sizes of 20–40 birds, depending on the species (Pickering et al., 1992). Additionally, the introduction of new individuals into an established flock can increase reproductive success in subsequent years beyond the benefit incurred from an increase in flock size alone (Rose et al., 2014; Stevens & Pickett, 1994). An even sex ratio increases both the probability of a flock reproducing and the degree of breeding success observed (King, 2008; Stevens, 1991). Although it is usually assumed that flocks reflect an even sex ratio, many captive flamingos are not sexed (King, 2008). Uneven sex ratios not only promote the formation of atypical partnerships (same-sex and triad partnerships), but a male-skewed sex ratio is also associated with colony unrest, higher rates of egg breakage, and lower reproductive success (King, 2006, 2008).

Weather conditions, particularly sufficient rainfall, play an important role in determining if and when flamingo reproduction will occur in captivity (Pickering, 1992; Stevens, 1991), although species-specific variations have been recorded (Pickering et al., 1992; Studer-Thiersch, 2000). This sensitivity likely stems from the fact that rainfall is often unpredictable and variable in natural flamingo habitats, yet rainfall provides the conditions necessary for nest building and the proliferation of small food organisms (Ogilvie & Ogilvie, 1986). Both high temperatures and prolonged photoperiod appear to stimulate reproduction in captive flamingos, even in flocks which are housed indoors (King, 2008). Conversely, prolonged periods of rainfall, cold, and cloud cover can inhibit reproductive activity (King, 2008; Rose et al., 2018). While suitable climatic conditions play an important role in the synchrony of reproductive events, they act in conjunction with flock dynamics and socially facilitated behaviors, such as courtship displays, to provide finer-scale synchrony and determine captive reproductive success (King, 2008). Ultimately, no single factor is essential for reproduction to occur, rather the effects of individual factors are cumulative once a threshold level of requirements is met (King, 2008).

The Flamingo Husbandry Guidelines (jointly developed by AZA and EAZA, in collaboration with the Wildfowl and Wetlands Trust in Slimbridge) provide recommendations to increase the probability of reproduction in captive flocks (Brown & King, 2005). These guidelines recommend each zoo only hold a single species of flamingo, with a minimum flock size of 20 birds for welfare purposes, and >40 birds to achieve a reasonable chance of reproductive success (Brown & King, 2005). These guidelines, which also consider many other factors and husbandry practices, represent the most promising solution to increase the sustainability of current ex situ flamingo populations, and their recommendations have been applied to the global ex situ management of all flamingo species.

While the implementation of revised management practices resulted in an improvement in overall flamingo reproductive success between 2005 and 2010, and in fact births now exceed deaths for the *Phoenicopterus* flamingos in EAZA institutions in most years (King & Bračko, 2014; ZIMS, 2020), ex situ populations are still unable to meet flock size recommendations, with many flocks still below 20 birds (Rose et al., 2014). The recommendations of the Flamingo Husbandry Guidelines were based on both existing evidence and realistic targets for zoos, however data available at the time came from a limited number of studies, often investigating single geographic regions, single institutional flocks, and/or were species-specific (Pickering et al., 1992; Stevens, 1991; Stevens & Pickett, 1994), with the recommended flock sizes being described as “somewhat arbitrary” (King & Bračko, 2014). Additionally, many studies fail to consider or are unable to separate the effects of species-specific differences in reproductive behavior, flock sex ratio and environmental conditions, making it difficult to draw general conclusions (Rose et al., 2014). Although the different flamingo species obviously share many commonalities, and some management practices can be applied to all, species-specific confirmations of the optimal flock size and composition necessary for reliable reproductive success are urgently required (King & Bračko, 2014; Sandri et al., 2018).

The globally shared records currently contained within the Zoological Information Management System (ZIMS), operated by Species360, provide a unique opportunity to investigate the relationship between flock size and reproductive success on a global scale. ZIMS is the largest real-time database of comprehensive and standardized information spanning more than 1200 zoological collections globally, and provides the number of institutions currently managing each species and both their current and historic population sizes (ZIMS, 2020). Here, for four flamingo species (*P. minor*, *P. chilensis*, *P. roseus*, and *P. ruber*) held in 540 zoological collections globally, we test how flock size and structure (proportion of females, unsexed individuals, and new individuals) influence reproductive success over the period 1990–2019. We also test whether captive reproductive success is influenced by latitudinal and climatic gradients, by incorporating measures of both temperature and precipitation. We implement a two-step modeling approach to assess both the probability of any individual in a flock reproducing in a given year, and then if reproduction occurred, the predicted number of chicks produced per flock. We also quantify how flamingo flock sizes have changed over the period 1990–2019. This is the most comprehensive assessment, to our knowledge, of the determinants of reproductive success in captive flamingos under a common modeling framework, providing the opportunity to reassess the recommendations of the Flamingo Husbandry Guidelines and identify potential species-specific differences in reproductive behavior. Results from this study have direct population management implications and could be directly incorporated into global flock management practices, improving the sustainability of ex situ flamingo populations.

2 | MATERIALS AND METHODS

We utilized current and historic globally shared zoological records from current and past Species360 member institutions (obtained via a Species360 research request) to investigate how flock size and structure influence reproductive success in captive flamingos. We combined demographic data with high resolution global climatic data within the same statistical modeling framework to gain a more complete view of the determinants of reproductive success in captive flamingo populations, while also revealing temporal trends in institutional flock sizes.

2.1 | Flamingo data

We obtained complete flamingo species holdings data across 540 zoological collections globally from ZIMS in April of 2019 (ZIMS, 2020). We screened the data for errors and inconsistencies (such as taxonomic ambiguity and unlikely longevity >99.9th percentile) and removed data as necessary. This resulted in the removal of 2.2% of the records available. Due to data quality and availability, our analyses were restricted to the period 1990–2019 and to the species *P. minor*, *P. chilensis*, *P. roseus*, and *P. ruber*.

We quantified and compared temporal trends in flock size for each species. We calculated the total number of hatches in each institution per year for each species. The flock size per institution per year between 1990 and 2019 was calculated from ZIMS data based on each individuals' hatch, death and transaction records (i.e., if the individual was translocated from one zoo to another). We subsequently calculated the total number of males, females, and unsexed individuals for each institutional flock for each year. To understand the importance of sexing individuals, we also calculated the proportion of unsexed individuals per flock per year. To test the effects of sex ratio, we calculated the proportion of females per flock per year. As many individuals remain unsexed, the proportion of females represents a conservative value for the true sex ratio of the flock, as it is likely that there are unsexed individuals which are female. We calculated the proportion of the flock in year t made up of individuals added in year $t\text{-}1$ (not including new birds hatched into the flock) to assess how the introduction of new individuals into a flock influences reproductive success in the subsequent year. A complete list of all calculated variables can be found in Table 1.

2.2 | Climatic data

We assessed the influence of climatic variables using data provided by WorldClim. The WorldClim database averages 19 different climatic variables derived from monthly temperature and rainfall values at a

TABLE 1 A complete list of the explanatory variables used

Variable	Description
Year	Current year (*t*)
Hatches	Number of birds hatched in year *t*
Flock Size	Flock size in year *t*
Proportion of Additions	The proportion of the flock in year *t* made up of additions from year *t-1* (not including new birds hatched into the flock)
Proportion of Unsexed	The proportion of the flock made up of unsexed individuals in year *t*
Proportion of Females	The proportion of the flock made up of female individuals in year *t*
MAP	Mean annual precipitation (mm)
MAT	Mean annual temperature (°C)
MAP Var	Mean annual variation in precipitation (MAP coefficient of variation)
MAT Var	Mean annual variation in temperature (MAT standard deviation)

Note: Mean annual temperature (MAT) is provided by WorldClim as °C multiplied by 10, and similarly mean annual variation in temperature as MAT standard deviation multiplied by 100. Both were divided (by 10 and 100, respectively) before modeling to avoid confusion in the units used.

1 km spatial resolution for the period 1970–2000 (Hijmans et al., 2005). Using geographic coordinates (latitude and longitude) we calculated mean annual temperature (MAT) and mean annual precipitation (MAP) for each institution. Given the sensitivity of flamingos to subtle environmental changes we also calculated measures of variation in both mean annual temperature (MAT standard deviation) and mean annual precipitation (MAP coefficient of variation).

2.3 | Modeling procedure

All data cleaning and analyses were carried out using the R program (version 3.4.3; R Core Team, 2017). To test for temporal trends in flock size between 1990 and 2019, flock size was modeled separately for each species using generalized linear mixed effects models with year included as a fixed effect, with random effects of the intercept and slope of year for each institution.

To assess reproductive success for each species, a two-step modeling approach was implemented for: (1) the probability of any individual in a flock reproducing in a given year, and if reproduction occurred, (2) the predicted number of chicks per flock. We modeled the probability of a flock reproducing as a zero-inflated binomial generalized linear mixed effects model. We modeled the number of predicted chicks per flock as a zero-truncated Poisson generalized linear mixed effects model. For both model structures, we included the country and institution nested within country as random effects. We tested for possible curvature in both flock size and the proportion of females using quadratic and cubic relationships. Two-way interactions between flock size and the proportion of unsexed, proportion of females and proportion of additions were also included, to better understand the combined effects of the different variables. All continuous explanatory variables were mean centered and expressed in units of standard deviation before modeling. Although comprehensive, this modeling procedure does not allow us to distinguish between whether the size of the flock increases an individual bird's probability of reproduction, or whether the individual probability of reproduction is constant for all birds and an increase in flock size just increases the chances that at least one bird will reproduce.

2.4 | Total and female analyses

Many individuals are unsexed, and as a result we were unable to calculate a reliable proportion of females for many flocks. We, therefore first modeled reproductive success excluding the proportion of females as an explanatory variable, replacing it with the proportion of unsexed individuals and its interaction with flock size to test whether uncertain sex ratio affected reproduction (540 current and past Species360 member institutions, that is, “Total Analysis”). A second analysis was performed on a subset of flocks for which at least 50% of the flock's sex was known (474 current Species360 member institutions, that is, “Female Analysis”), using the proportion of females, its quadratic term, and its interaction with flock size as explanatory variables instead of the proportion of unsexed individuals, in addition to all of the other variables included in the Total Analysis. Higher thresholds were also tested, however, 50% was the highest cut-off value which allowed for model convergence. Total and Female Analyses revealed quantitatively similar results, despite the reduction in sample size for the Female Analysis. Therefore, only the additional female variables of the Female Analysis are reported in the results, as all other relationships were derived from the Total Analysis due to its higher statistical power.

2.5 | Model selection

Based on the a priori hypothesized relationships, a maximal model for reproduction containing all possible explanatory variables (flock size, year, proportion of additions, proportion of unsexed, and the four climatic variables), and selected two-way flock size interactions (with the proportion of additions and the proportion of unsexed), was generated for each species. Model selection was conducted using AICc values on all subsets of the maximal model, with a threshold of more than two AICc units lower than the nearest competing model being considered sufficient for model selection (Burnham & Anderson, 2002). This was repeated for the Female Analysis, replacing the proportion of unsexed individuals with the proportion of females per flock, its quadratic term, and its interaction with flock size. The original maximal and final species-specific models for both the “Probability of Reproduction” and “Number of Chicks” models are shown in Supporting Information: Tables S1 and S2, including both the Total and Female Analyses. Residual diagnostic plots investigating overdispersion and zero-inflation parameters were generated to confirm the validity of all final models.

3 | RESULTS

3.1 | Flamingos in zoos and aquariums

As of October 2020, there were a total of 19,773 extant flamingos across the Species360 member institution network, spanning 474 institutions in 54 countries (Figure 1; Table 2). Species-specific institutional distributions can be found in the Supporting Information (Supporting Information: Figures S1–S4). *P. chilensis*, *P. roseus*, and *P. ruber* all have similarly large ex situ populations (ranging from 5528 to 6928 individuals), whereas *P. minor* has a much smaller extant ex situ population of 1422 individuals. This bias is also reflected in the total number of hatches for each species between 1990 and 2019 (Table 2). The sex ratio of ex situ flamingo populations is relatively even for *P. chilensis*, *P. roseus*, and *P. ruber*, however *P. minor* shows a male bias (55.5% of all individuals). Importantly, 23.3% (4601/19,773 birds) of individuals have not yet been sexed.

3.2 | Reproductive success

Flock size has a strong positive influence on the probability of reproduction and the predicted number of chicks per flock in all four species of flamingo analyzed ($p < .05$ for all relationships; Figures 2 and 3). Species-specific "Probability of Reproduction" and "Number of Chicks" model results (showing all standardized effect sizes for both the Total Analysis and Female Analysis) are reported in Table 3. There are notable increases in the probability of reproduction between flock sizes of 40 to 100+ individuals in all species (Figure 2). The currently recommended flock size of 40 individuals results in a probability of

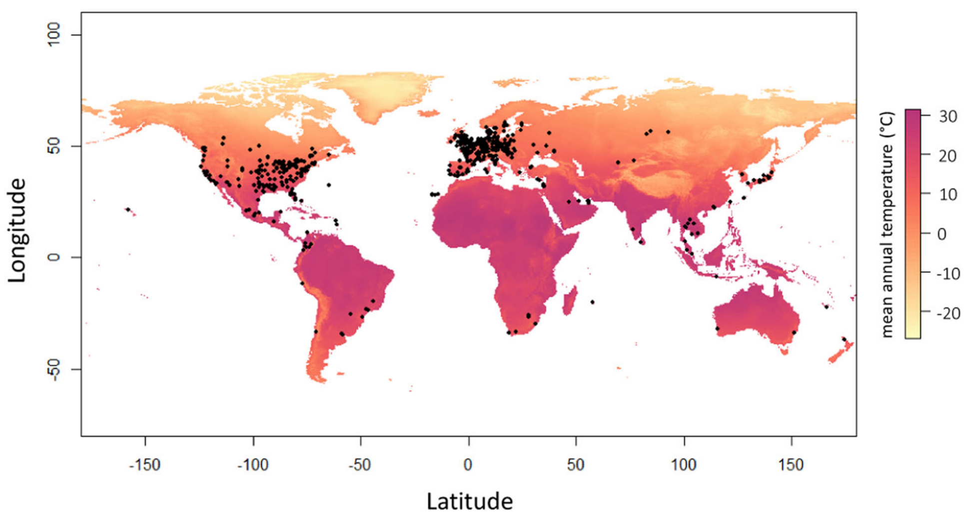

FIGURE 1 The global distribution of current Species360 member institutions containing flamingo flocks. These are presented on a global map showing mean annual temperature at a resolution of 1 km. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Summary statistics for each flamingo species maintained within the Species360 member institution network for the period 1990–2019

	Living population (2019)						
Species	M	F	U	Total	Current institutions	Institutions with hatches (1990–2019)	Total hatches (1990–2019)
Phoeniconaias minor	789	396	237	1422	58	18	285
Phoenicopterus chilensis	2107	1957	1464	5528	177	172	5722
Phoenicopterus roseus	2555	2714	1659	6928	186	122	6594
Phoenicopterus ruber	2360	2255	1240	5855	172	142	6506
Phoenicoparrus andinus	14	18	1	33	2	3	7
Phoenicoparrus jamesi	2	5	0	7	1	1	6

Note: Living population as of 2019: M, male; F, female; U, unsexed individuals. Summary statistics for *P. andinus* and *P. jamesi* are shown for comparison. Institutions may currently house, or have previously housed, more than one flamingo species.

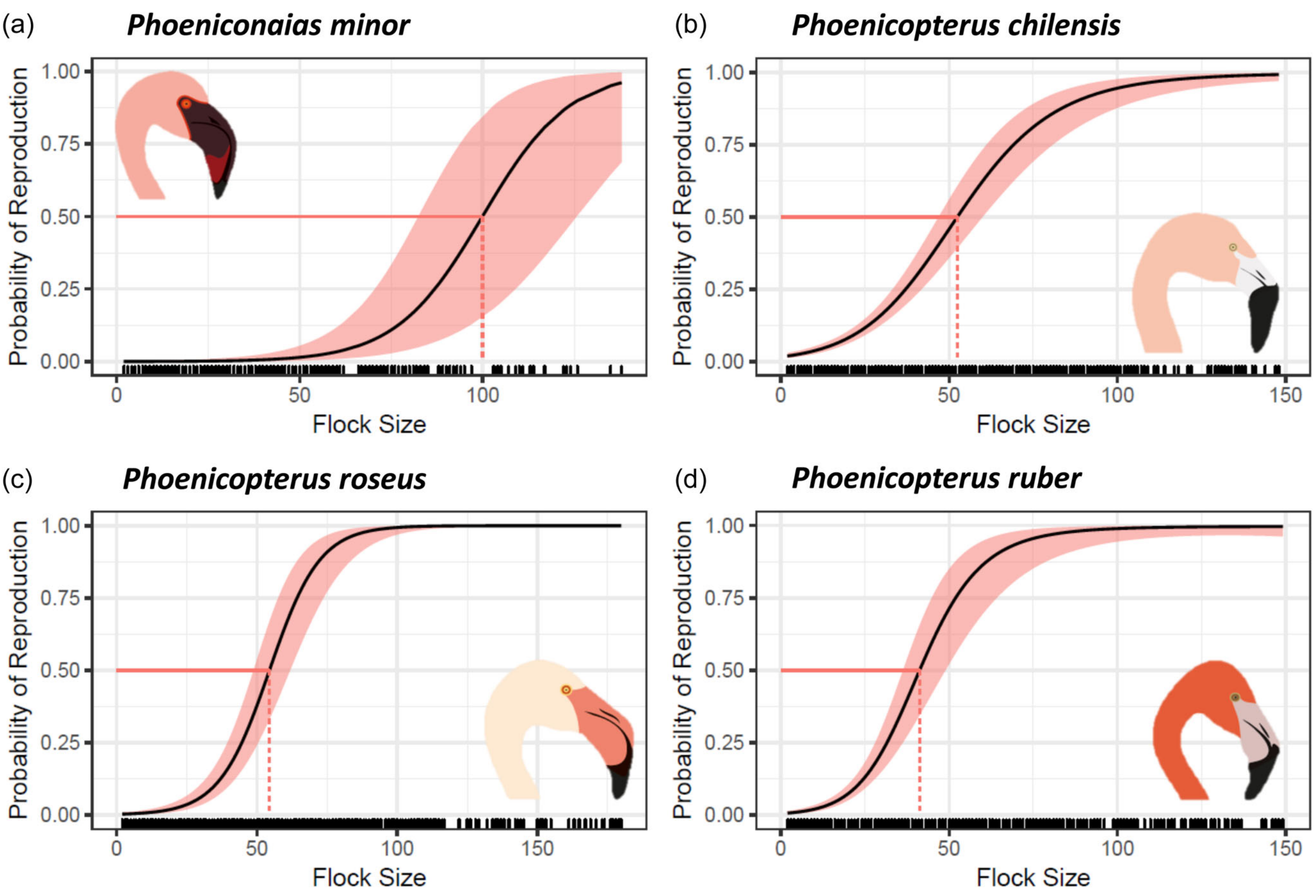

FIGURE 2 The relationship between ex situ flock size and the probability of reproduction for *Phoeniconaias minor* (a), *Phoenicopterus chilensis* (b), *Phoenicopterus roseus* (c) and *Phoenicopterus ruber* (d) between 1990 and 2019. Curved black lines represent predicted values from the Total Analysis on the original response variable scale, and shaded areas represent 95% confidence intervals. Dashed lines represent the flock size necessary to achieve a 50% probability of reproduction. Predicted values shown are based on different flock sizes, with all other explanatory variables kept constant and set to their mean values. [Color figure can be viewed at wileyonlinelibrary.com]

reproduction of 0% for *P. minor*, 29% for *P. chilensis*, 16% for *P. roseus*, and 46% for *P. ruber*. The flock size necessary to achieve a 50% probability of reproduction is 100 for *P. minor*, 52 for *P. chilensis*, 54 for *P. roseus*, and 41 for *P. ruber*. There is also an increase in the number of chicks produced with flock size ($p < .05$ for all relationships; Figure 3). Although we see decreases in the number of chicks produced at very large flock sizes, this likely stems from the limited number of institutions with flock sizes of more than 100 individuals and the direct management interventions they deploy to prevent overpopulation.

An even sex ratio, or one that is female biased, enhances both measures of reproductive success in *P. minor* and *P. roseus* (see Figure 4 for an example; $p < .05$). For *P. chilensis*, the probability of reproduction is consistently high across nearly all sex ratios, but very female biased sex ratios may have reduced probabilities of reproduction (Supporting Information: Figure S7b). In contrast, an even sex ratio, or female biased sex ratio, enhances the number of chicks produced in smaller *P. chilensis* flocks (<35 individuals) (Supporting Information: Figure S16). The addition of new individuals to a flock increases the number of chicks produced per flock (*P. chilensis*, *P. roseus*, and *P. ruber*; Figure S14), but has little influence on the probability of reproduction (except in *P. ruber*). Significant synergistic interactions of flock size with both the proportion of females and the proportion of new individuals per flock were also found to influence both measures of reproductive success. For example, the benefit of adding new individuals to a *P. roseus* or *P. ruber* flock, in terms of the number of chicks produced, is enhanced at larger flock sizes ($p < .05$; Figure 5a,b).

High mean annual precipitation lowers the probability of reproduction (*P. chilensis* and *P. ruber*) and the number of chicks produced (*P. chilensis* only). MAT appears to have no effect on the probability of reproduction, however, a significant positive relationship exists between the number of chicks produced and higher MATs (*P. chilensis*; $p < .05$). A summary of the flock structure and climatic variables which influence the probability of reproduction and the number of chicks produced in ex situ flamingo flocks is shown in Figure 6. Detailed species-specific findings are reported in the Supporting Information: Note S1 and Figures S1–S19. All maximal and final species-specific Total and Female Analysis models can be found in the Supporting Information (Supporting Information: Tables S1 and S2), with associated standardized effect sizes, standard errors, and *p*-values shown in Supporting Information: Tables S3–S10.

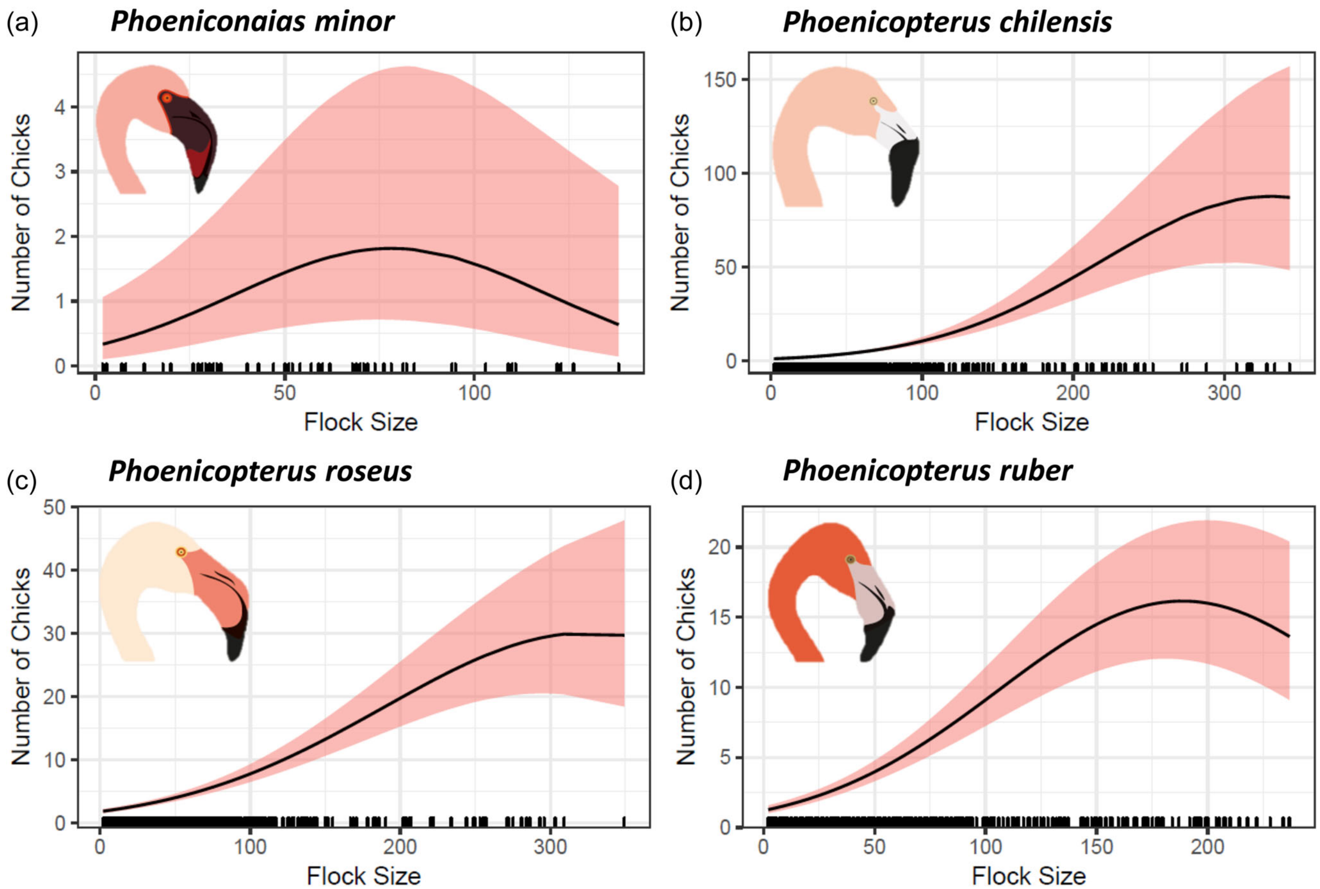

FIGURE 3 The relationship between ex situ flock size and the number of chicks produced for *Phoeniconaias minor* (a), *Phoenicopterus chilensis* (b), *Phoenicopterus roseus* (c) and *Phoenicopterus ruber* (d) between 1990 and 2019. Curved black lines represent predicted values from the Total Analysis on the original response variable scale, and shaded areas represent 95% confidence intervals. Predicted values shown are based on different flock sizes, with all other explanatory variables kept constant and set to their mean values. [Color figure can be viewed at wileyonlinelibrary.com]

3.3 | Temporal patterns

Overall flock sizes of *P. chilensis*, *P. roseus*, and *P. ruber* have significantly increased over time ($p < .05$ for all relationships; Figure 7; Supporting Information: Table S11), however, the majority of flocks are still well below the recommended flock size of 40 birds. Flock size is very consistent between these three species, with an increase in flock size from a mean of 12.70 (±2.21 S.D.) birds in 1990 to 28.60 (±2.34 S.D.) birds in 2019 observed across all species. Although flock sizes of *P. minor* have also increased over time, from a mean of 14.37 in 1990 to 17.80 in 2019, this was nonsignificant ($p = .063$).

4 | DISCUSSION

Results from this study show a significant reproductive benefit, for all flamingo species assessed, of housing flocks greater than 40 individuals, with the highest levels of reproductive success observed in flocks of approximately 100+ individuals. We also confirm the importance of an even sex ratio for some species, and provide the first statistical evidence that adding new individuals into an existing flock can increase reproductive success. However, we also reveal novel and important synergisms between flock size, sex ratio, and the addition of new individuals into an existing flock, providing potential management solutions to help mitigate the effects of smaller flock sizes.

We confirm for four flamingo species commonly kept in zoos and aquariums, the positive effect of flock size on both the probability of a flock reproducing and the number of chicks produced. However, species-specific differences must be considered and incorporated into management recommendations. While we found that reproductive success is indeed enhanced in flocks of >40 individuals, reinforcing the flock size recommendations of the 2005 Flamingo Husbandry Guidelines (Brown & King, 2005), a flock size of just 40 individuals results in a probability of reproduction of just 0%–46% for the four species. Rather than viewing 40 individuals as the target, this is an absolute minimum flock size if reproductive success is the institutional-specific goal of ex situ management, and we suggest that significantly larger flocks should be maintained wherever possible to achieve greater reproductive success. Flock sizes of between 41 and 54 birds appear necessary to achieve a 50% probability of reproduction in any year, however for *P. minor* the required flock size

TABLE 3 A summary of the standardized effect sizes for both the Total and Female Analyses, considering both the probability of reproduction and the number of chicks produced in *Phoeniconaias minor*, *Phoenicopterus chilensis*, *Phoenicopterus roseus*, and *Phoenicopterus ruber* flocks between 1990 and 2019

Species	Intercept	Flock size	(Flock size)^2	Prop. females	(Prop. females)^2	Flock size * prop. females	Year	Prop. new	Flock size * prop new	Prop. Unsexed	Flock size * prop. unsexed	Mean annual precipitation (MAP)	Mean annual temperature (MAT)	MAP Var.	MAT Var.
Probability of reproduction															
Total analysis															
P. minor	**−6.70*****	**1.81*****	-				**0.58****	-	-	**−1.41***	-	-	-	-	-
P. chilensis	**−1.93*****	**2.46*****	**−0.18*****				**−0.37*****	-	-	0.04	**−0.35***	**−0.25***	-	−0.18	-
P. roseus	**−2.82*****	**4.16*****	-				-	-	-	−0.09	-	-	−0.30	-	-
P. ruber	**−1.82*****	**3.82*****	**−0.49*****				−0.28	**0.37*****	-	0.02	0.32	**−0.57****	-	−0.28	-
Female analysis															
P. minor	**−6.35*****	**1.81*****	-	**1.34*****	-	-	**0.63****	-	-			-	-	-	-
P. chilensis	**6.57*****	**12.80*****	-	−0.30	**−0.20***	-	**−0.33***	**30.29*****	**36.42*****			**−0.31***	-	-	-
P. roseus	**−1.67*****	**4.39*****	**−0.47*****	−0.06	**−0.52****	−0.55	-	-	-			-	-	−0.12	-
P. ruber	**−1.56*****	**3.46*****	**−0.45*****	0.21	-	-	-	**0.33*****	-			-	-	-	**0.40***
Number of chicks															
Total analysis															
P. minor	0.48	**0.39***	**−0.32****				**0.48****	-	-	-	-	-	-	-	-
P. chilensis	**1.28*****	**1.07*****	**−0.09*****				-	**0.22*****	-	**−0.10***	-	**−0.14****	**0.17*****	-	-
P. roseus	**1.48*****	**0.69*****	**−0.06*****				**0.14****	**0.13*****	**0.03****	-	-	-	-	-	-
P. ruber	**1.39*****	**0.83*****	**−0.12*****				-	**0.22*****	**0.07*****	-	-	-	-	-	-
Female analysis															
P. minor	**0.85***	**0.95*****	**−0.29****	0.01	**0.294*****	**0.702*****	-	-	-			-	-	-	-
P. chilensis	**1.27*****	**1.05*****	**−0.12*****	−0.02	-	**−0.10****	-	**0.16*****	-			-	-	-	-
P. roseus	**1.57*****	**0.63*****	**−0.37*****	**−0.12*****	**−0.04***	-	**0.16****	**0.10*****	-			-	-	-	-
P. ruber	**1.34*****	**0.84*****	**−0.12*****	-	-	-	-	**0.27*****	-			-	-	-	-

Note: Statistical significance is denoted by an asterisk (*), with $p < .05$ (*), $p < .01$ (**) and $p < .001$ (***). Dashes indicate variables which were not retained in the final models, and blank gray cells represent variables not included in the original maximal model. Prop.Females, proportion of females; Prop.New, proportion of additions; Prop.Unsexed, proportion of unsexed; MAP Var., mean annual variation in precipitation; Mat Var., mean annual variation in temperature. Note that these effect sizes are from the linear predictor of the standardized explanatory variables, and therefore the sign of the parameters needs to be interpreted with care, particularly where quadratic effects are present. See Figure 4, Supporting Information: Figure S7a,b for predictions from the model to aid in interpretation.

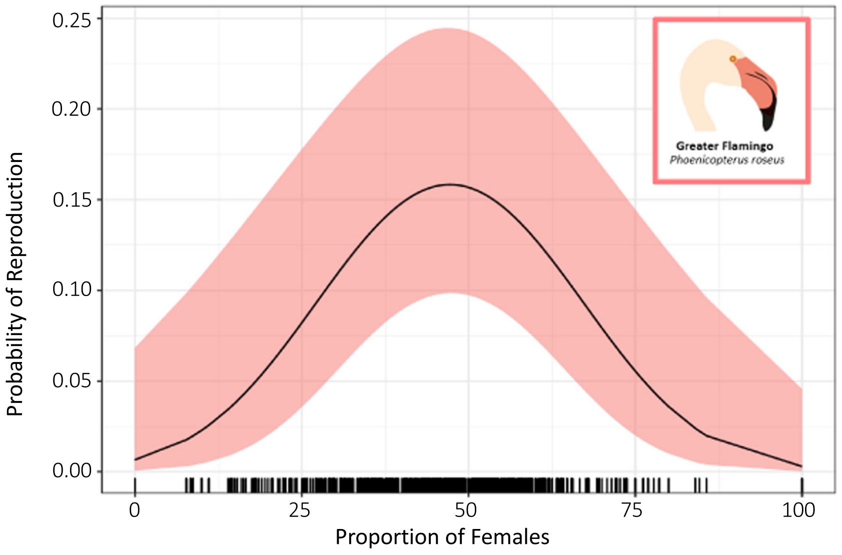

FIGURE 4 The relationship between the proportion of females in a flock and the probability of reproduction for *Phoenicopterus roseus* between 1990 and 2019. The curved black line represents predicted values from the Female Analysis on the original response variable scale, and the shaded area represents 95% confidence intervals. Predicted values shown are based on different proportions of females in a flock, with all other explanatory variables kept constant and set to their mean values. Black lines on the *x*-axis reflect the distribution of the data. [Color figure can be viewed at wileyonlinelibrary.com]

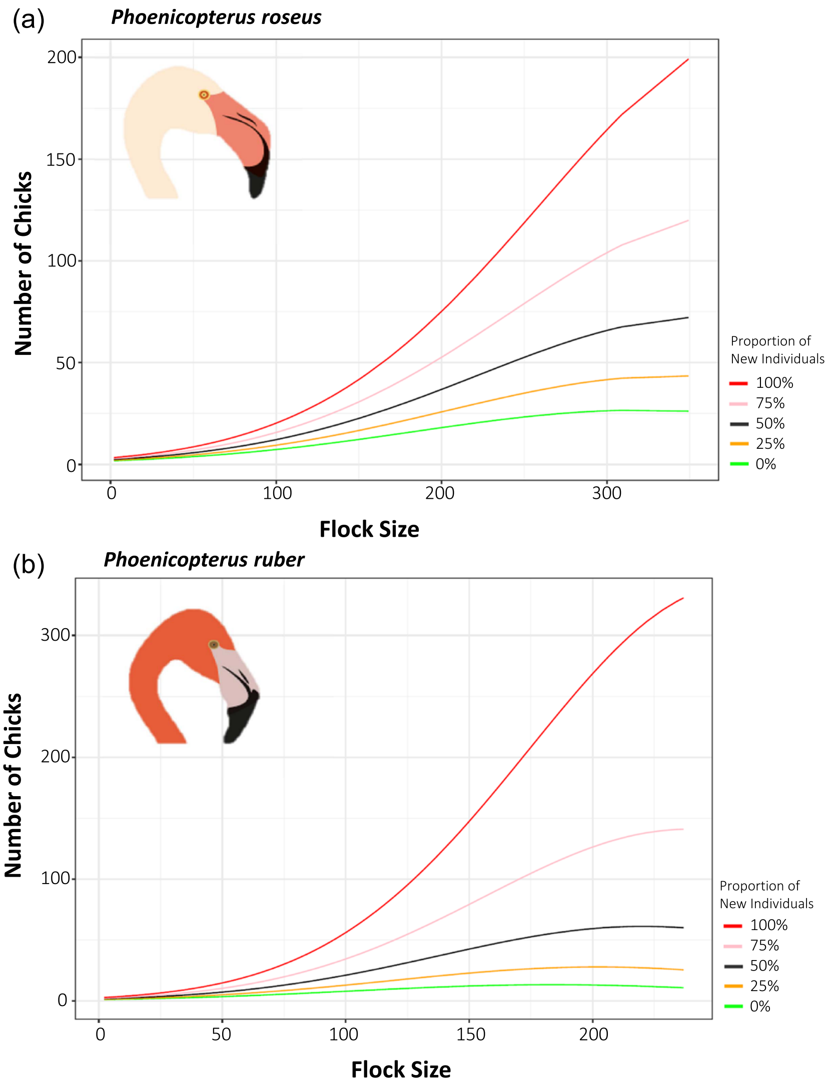

FIGURE 5 The relationship between ex situ flock size and the number of chicks produced for *Phoenicopterus roseus* (a) and *Phoenicopterus ruber* (b) at varying proportions of new additions per flock between 1990 and 2019. Colored lines represent predicted values from the Total Analysis on the original response variable scale. [Color figure can be viewed at wileyonlinelibrary.com]

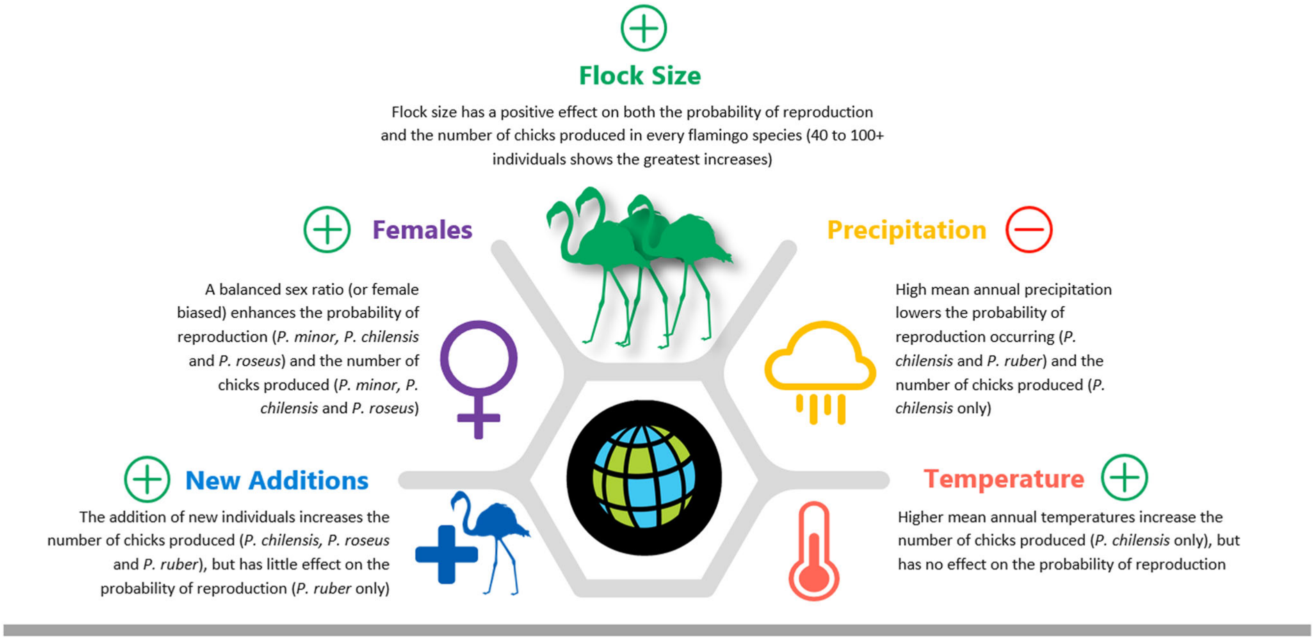

FIGURE 6 A summary of the flock structure and climatic variables which influence both the probability of reproduction and the number of chicks produced in ex situ flamingo flocks of *Phoeniconaias minor*, *Phoenicopterus chilensis*, *Phoenicopterus roseus*, and *Phoenicopterus ruber*. Green circles denote positive relationships, whereas red circles denote negative relationships. [Color figure can be viewed at wileyonlinelibrary.com]

increases to 100 birds, with a negligible probability of reproduction in flocks of less than 50 individuals. Flamingos are some of the most popular species in zoo collections, and an increase in flock size may also help to increase both visitor numbers and in situ conservation investment (Mooney et al., 2020).

We confirm that both an even sex ratio and/or the introduction of new individuals positively influence reproductive success in some species, consistent with previous studies (King, 2008; Stevens & Pickett, 1994; Stevens, 1991), however, the influence of both sex ratio and flock additions can vary depending on the flock size context. While we found that climatic variables in general play a limited role in determining captive reproductive success, high annual rainfall is negatively associated with reproductive success, consistent with King (2008). We encourage more detailed assessments incorporating seasonality and photoperiod to potentially reveal more nuanced relationships not identified here (Wilson et al., 2019).

Despite the majority of contemporary flocks still being below the previously recommended minimum flock size of 40 birds, important synergistic interactions of flock size with both the proportion of females and the proportion of new individuals per flock provide an important and underappreciated mechanism to mitigate the effects of small flock sizes and encourage reproduction through management practice. Although the effect is greatest at larger flock sizes, the introduction of new individuals into small *P. ruber* flocks can increase reproductive success the following year, compared to similarly sized flocks with no new individuals (Figure 5b). This relationship is mirrored in *P. roseus* (Supporting Information: Figure S19). Based on this evidence, we recommend that institutions consider periodically moving individuals to help encourage reproduction, however, more work is needed to identify how often this should happen and the possible welfare consequences of regularly moving individuals. This movement of birds should be done as part of co-operative population management between zoos and aquariums, and coordinated by the relevant Taxon Advisory Groups of regional zoo associations. Further research is also needed on the possibility of separating and reintroducing existing flocks before the breeding season to encourage reproduction, particularly where physical transfer of individuals is not possible (Shannon, 2000). Reproductive success can be enhanced in smaller flocks of *P. minor*, *P. chilensis*, and *P. roseus* through an increase in the proportion of females toward an even sex ratio. This is particularly important in flocks of *P. minor*, where an overall male bias exists and minimum flocks of 150 birds are required for reliable reproduction (Table 2; Figure 2a). Here, an increase in the proportion of females to achieve an even sex ratio can decrease the flock sizes necessary to achieve higher numbers of chicks per flock (Supporting Information: Figure S15).

The presence of unattached males is known to be disruptive to colony dynamics and can result in higher rates of egg breakage (King, 2006, 2008). Therefore, an approach toward an even sex ratio should also be considered a priority from an animal welfare perspective, and population managers should increase their efforts to sex all currently unsexed individuals. Similarly, the extremely high prevalence of monogamy and long-term pair bonds in captive flamingos, despite their rarity in the wild, is likely a direct result of limited mate choice (King, 2006; Rose et al., 2014). An increase in both flock size and the periodic introduction of new individuals could potentially provide a tool to promote wild-type behavior in captive settings, providing greater opportunities for mate choice

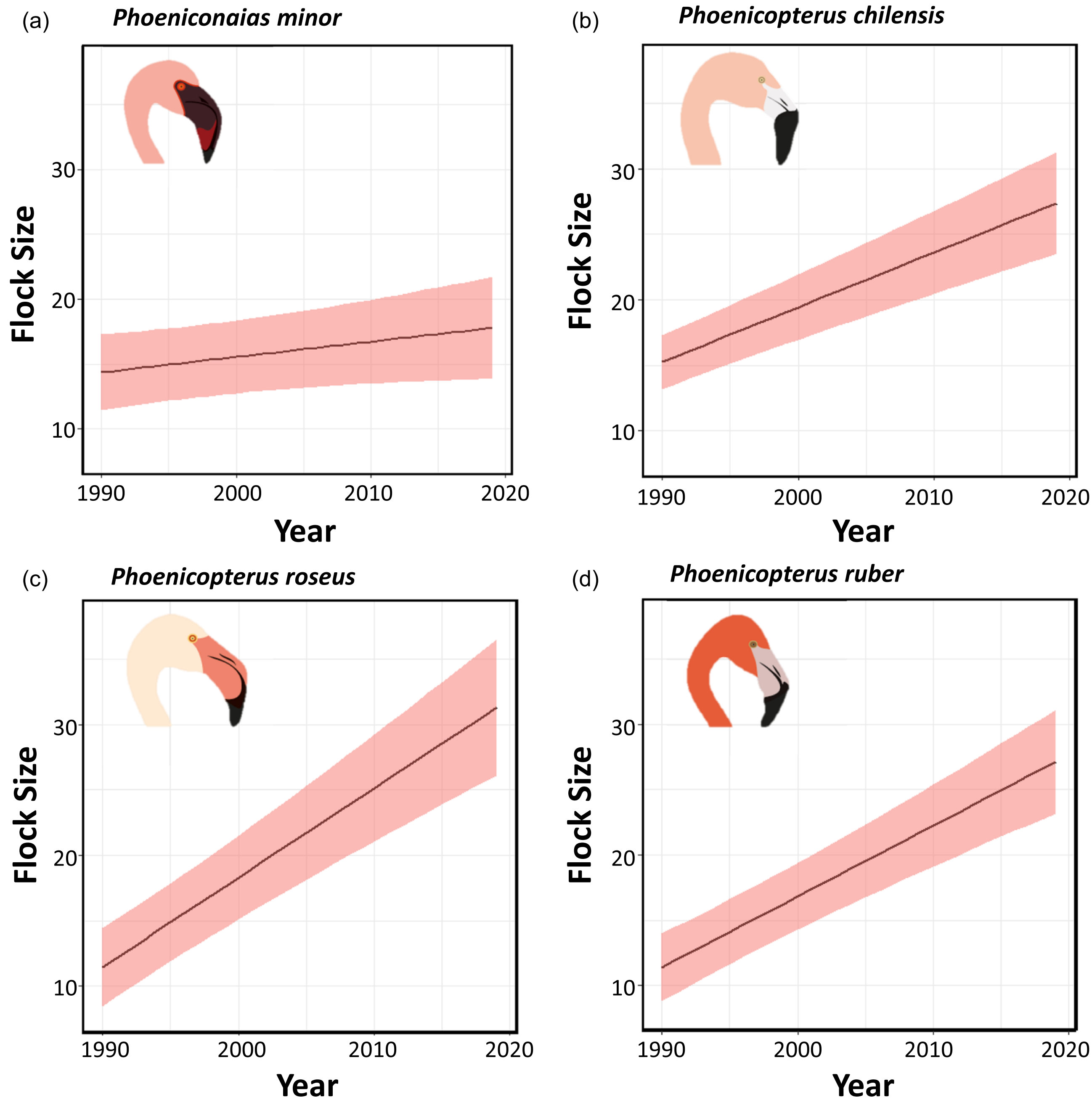

FIGURE 7 Changes in flock sizes for *Phoeniconaias minor* (a), *Phoenicopterus chilensis* (b), *Phoenicopterus roseus* (c), and *Phoenicopterus ruber* (d) between 1990 and 2019. Black lines represent predicted values and shaded areas represent 95% confidence intervals. [Color figure can be viewed at wileyonlinelibrary.com]

and allowing for enhanced social stimulation in the form of synchronized group displays, pair formation, and nesting (Rose et al., 2014; Stevens, 1991). Further work is required in this area, and greater consideration needs to be given to the behavioral and social dynamics within flocks, how they influence reproductive success, and how management practices influence these dynamics (King, 2006; Shannon, 2000).

Although comprehensive, this study is unable to capture important determinants of reproductive success, such as institutional management practices, enclosure design, wing condition, behavior, diet, and time activity patterns, all of which warrant further investigation (Sandri et al., 2018). For example, the wing condition of male birds (full-winged, wing-clipped, or pinioned) is arguably the main cause of male infertility, with up to 75% of traditionally pinioned males unable to successfully copulate (King, 2008). Although flamingos are not currently under any known contraceptive or management practice that would prevent reproduction, deliberate institutional interventions to limit reproduction in very large flocks have been known to occur and may explain why our results show decreases in reproductive success for some species at very large flocks (ca. 200+ individuals) (Rose *pers. obs.*). While these management issues are not in the scope of the current study, they impact the results presented here, and are dealt with in greater detail as part of the Flamingo Husbandry Guidelines (Brown & King, 2005; King & Bračko, 2014).

Ultimately the implementation of these recommendations will fall upon regional and institutional population managers. Fortunately, the popularity of flamingos has made it easier to gain momentum for management improvements compared to other avian species, with the majority of institutions willing to make necessary management changes to increase population sustainability (King & Bračko, 2014). However, this popularity has also made it clear that certain institutions are reluctant to relocate their flamingos to other institutions (King & Bračko, 2014). In addition, limited space, lack of standardized husbandry practices, and the need for improved fulfillment of breeding and transfer recommendations all pose significant problems for currently managed ex situ populations (Wilson et al., 2019). Nearly 40% of AZA co-operatively managed colonial bird breeding programs state that they require additional space if population sustainability goals are to be met (Wilson et al., 2019). If all flamingo populations reach the minimum recommended population sizes and reproductive rates necessary, population sustainability will only continue if these high reproductive rates are maintained, which will only occur if significantly more space is made available, ideally in climatically suitable regions. Similarly, the recommendation to periodically move individuals between flocks may encounter significant obstacles, with 33% of all co-operatively managed AZA programs having reported issues with the fulfillment of breeding and transfer recommendations (Wilson et al., 2019). Population managers are aware of these issues and over the last 10 years the AZA Avian Scientific Advisory Group has held several meetings to specifically troubleshoot issues relating to the breeding and population management of lesser flamingos. One specific recommendation was to create all-male colonies at designated institutions to help balance the sex ratio of breeding flocks and manage the current male bias in the population. This was successfully achieved through the co-operation of participating institutions, representing a promising example that these obstacles can be overcome to help improve ex situ population management and sustainability moving forward (Conrad, 2016; Putnam, 2019).

The sustainable management of ex situ flamingo populations is only one component of the global effort to conserve flamingos. Through this thorough exploration of the population dynamics and climatic conditions underlying captive flamingo reproduction we hope to add to the global body of knowledge of species-specific flamingo biology and ecology. The work presented here could be used to help understand the population dynamics of wild flamingos, particularly as their populations and habitats become more fragmented due to anthropogenic threats and encroachment. Sharing this knowledge, and potential mitigation measures, with in situ partners is in line with the integrated approach to species conservation encouraged by the IUCN CPSG. Their "One Plan Approach" promotes the exchange of knowledge and collaboration between all parties involved in the conservation of a species (Byers et al., 2013). We believe further collaboration between all stakeholders is necessary to not only provide guidance to institutions on management, research, and education messaging priorities, but also to identify opportunities for the integration of in situ and ex situ conservation efforts moving forward. This could include the potential future use of ex situ populations for bolstering of in situ populations, as has been done for the African penguins (*Spheniscus demersus*) (Schwitzer et al., 2013). Given ongoing biodiversity loss, connecting the power of globally shared ex situ records, and management expertise, with in situ conservation practitioners, is critical to the identification of the most efficient conservation and management strategies necessary to ensure that both in situ and ex situ populations remain sustainable into the future.

5 | CONCLUSION

In conclusion, we recommend that ex situ institutions significantly increase the size of their flamingo flocks to between 50 and 100 individuals, depending on the species, and ensure they consist of an even sex ratio. We also recommend periodically moving individuals between institutions to help encourage reproduction and mitigate the effects of smaller flock sizes. If the management actions presented in this study are followed through international collaboration and co-operative population management, then the sustainability of ex situ flamingo populations can be enhanced, from which both in situ and ex situ conservation actions can arise.

AUTHOR CONTRIBUTIONS

Andrew Mooney and J. Andrew Teare developed the concept of the manuscript. Andrew Mooney, Johanna Staerk, and Simeon Q. Smeele collected the data. Andrew Mooney undertook the analysis and drafted the text in consultation with all authors. Andrew Mooney produced the tables and figures. All authors contributed to the writing of the manuscript and gave final approval for publication. This study used globally shared zoological records and no local data collection was required, however, the geographical distribution of the authorship team broadly represents the major regions included in this study.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Anonymized data files for each species, and associated metadata, are available from https://doi.org/10.5281/zenodo.7504076. In line with the FAIR data principles, the data are made available under the following license: Creative Commons Attribution 4.0 International (CC BY 4.0).

ETHICS STATEMENT

Not applicable.

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SUPPORTING INFORMATION

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

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