

Research article

King penguins in zoos: relating breeding success to husbandry practices

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Abstract

As global climate change warms the Southern Ocean, wild king penguins (*Aptenodytes patagonicus*) may face drastic population declines in the future. Moreover, the captive breeding programme in Europe is currently unsustainable and it is thus imperative to determine what is required for the successful breeding of king penguins. A questionnaire was used to assess the husbandry practices and breeding success of 12 American and European zoos. Overall, a positive relationship was found between yearly egg productivity and density of king penguins held in enclosures in different zoos. All zoos examined showed male-biased adult sex ratios. Yearly egg productivity was negatively related to the deviation from an even sex ratio. Mean hatching success was greater in zoos performing outside walks with king penguins than in those that did not. Based on records over 40 years, the population of the sustainably breeding Basel Zoo in Switzerland was modelled using stage-based matrix models to gain an insight into its breeding success. Years of medium colony size (density of 0.25 to 0.38 individuals per m²) displayed a larger growth rate than years with high or low colony size, and years with equal sex ratios showed a higher growth rate than those with male-biased or female-biased sex ratios. The results suggest zoological institutions should focus on increasing density and strive toward equal sex ratios within king penguin populations to maximise breeding success. Where possible, adding outside walks should also be taken into consideration.

Introduction

Ex-situ conservation could serve as a crucial tool in securing a species' place on our planet in the future (Glowka et al. 1994). Although the king penguin (*Aptenodytes patagonicus*) is currently listed by IUCN as a species of least concern (IUCN 2013), this could alter in the future, especially with advancing climate change. Polar habitats have been particularly strongly affected by increasing temperatures (Solomon et al. 2007) and an accelerated warming of the Southern Ocean can be expected (Mayewski et al. 2009; Liu and Curry 2010). Studies based on current estimates of temperature changes by the Intergovernmental Panel on Climate Change (IPCC) suggest shifts in king penguin foraging ranges and consequently possibly drastic population declines putting king penguins at risk of extinction (Le Bohec et al. 2008; Péron et al. 2012). This is complicated by the species' complex breeding cycle, which extends over more than a year, and a long generation time (Weimerskirch et al. 1992), neither of which are favourable

to microevolution within a short period, thus reducing the chances of selective adaptation (Gienapp et al. 2008).

Because of this risk of dramatic drops in wild king penguin population numbers, it is necessary to determine what is required for breeding success in captivity, so that ex-situ breeding programmes might one day help conserve this species in conjunction with in-situ measures. Focusing on optimising breeding success within zoo networks, such as the European Association of Zoos and Aquariums (EAZA), also eliminates the need for penguins or eggs to be imported from the wild or more successfully breeding overseas zoos, which is associated with economically costly airline transport. At present, these imports from overseas (mainly from North American zoos) are keeping the European captive king penguin population at the desired size. Without them, the population would have decreased by 25% between 1999 and 2008, and it has been estimated that within 50 years the population could decline by as much as 75% without imports from outside the EAZA population (Elliot and Talbot 2009). It is therefore crucial for networks

of zoological institutions to become self-sufficient breeders. Moreover, it is advantageous to have many zoos within a network be successful breeders so that different zoos may exchange individuals to maximise genetic diversity within zoo populations. Lacy (2013) suggests that in order to achieve sustainability, it is imperative for zoo populations to be managed as components of a metapopulation.

One population within Europe that exhibits continuous breeding success is that of Basel Zoo, Switzerland. This zoo has been holding king penguins since 1953 and has been successfully breeding (defined here as not just producing eggs, but having chicks achieve fledgling age of one year) since 1959. The reason for this success has not so far been identified. Thus, the objective of this study was to examine what factors define a sustainably breeding king penguin population by comparing breeding success and husbandry practices internationally, and modelling the population at Basel Zoo based on breeding records over 40 years. Only a few recent studies have investigated optimal conditions for holding penguins (Blay and Côte 2001) and even fewer, if any, have simulated captive penguin populations using stage-based matrix models.

Matrix models are valuable tools in determining how populations might develop in the future. In contrast to unstructured models, matrix models are structured models taking differences among individuals in terms of their survival and fecundity into account (e.g. Akçakaya et al. 1999). They partition populations into discrete age, size or stage classes with class-specific demographic parameters (survival, fecundity). Therefore, they add detail to models of population dynamics by accounting for differences in demographic parameters among individuals in different stages (Caswell 2001). Matrix models are often used in ecology to model population growth and assess whether a population will subsist or go extinct based on estimates of demographic parameters. Furthermore, such models can demonstrate how external factors affect demography. For populations held in captivity, influences of management actions or environmental fluctuations, such as a disease outbreak, can be simulated (Faust et al. 2004). Faust et al. (2003) further argue that when modelling managed populations such as those in zoos, it is beneficial to use stage-based models, as they utilise mortality and fecundity rates for naturally occurring stages instead of different rates for each age. As part of the present study, the king penguin population at Basel Zoo was examined using stage-based matrix models to provide a more detailed insight into this population's breeding success.

Methods

Husbandry practices and breeding success among zoos

A questionnaire was designed to obtain information on population dynamics and husbandry practices from zoological institutions. Zoos were personally visited or contacted via e-mails to the responsible curator or main keeper of king penguins. A total of 12 institutions holding king penguins, nine European and three from the United States, provided all the necessary information required to participate in this study. Zoos that were restricting breeding were excluded from the start.

The questionnaire targeted information about the population itself, breeding success, enclosure specifics, cohabiting species and enrichment, as well as breeding-related husbandry practices (see Supplementary Table S1). Zoos were requested to supply an ARKS or ZIMS report for the years 2007–2012, which gave information on population dynamics. In addition, the questionnaire asked zoos to give yearly numbers of eggs laid from 2007 to 2011. The enclosure section of the questionnaire included questions about the surface area of land available and the number of individuals of any other species cohabiting within the enclosure. Questions about husbandry practices were also posed, including the nature

of any shows king penguins were involved in, time spent outside, frequency of disinfectant and fungicide use, and presence of natural light. Lastly, participating zoos were asked whether eggs were incubated by the parents or artificially in an incubator and whether chicks were parent or hand reared.

Breeding success was based on three parameters presented by Blay and Côte (2001), which are averages across the five years studied: mean egg productivity (number of eggs laid per number of adult individuals in one year), mean chick productivity (number of chicks hatched that would fledge the following year per number of adult individuals in one year), and mean hatching success (number of chicks hatched per number of eggs laid in one year). As a fourth breeding parameter, mean chick survival was defined as the number of chicks that would fledge per number of chicks hatched in one year. The term 'adult individuals' refers to males, females and penguins of unknown sex above the age of three.

Statistical analyses were performed in R (R Development Core Team 2011). The possibility of density dependence was assessed using a linear model in which the independent variable, king penguin density, was defined as the number of individuals (adults, subadults and chicks) per m² of land in the enclosure. The four different breeding parameters were tested as dependent variables. Total density (including all individuals of other species of birds sharing the same enclosure) was also tested as an independent variable. Wuppertal Zoo was excluded from all density analyses, as their king penguin population moved to a new enclosure in the middle of the five-year period assessed. Wilcoxon rank sum tests were used to compare mean hatching success and mean chick survival between zoos relying mostly on artificial incubation and/or hand rearing, respectively, as opposed to mostly leaving eggs and chicks with their parents. Other husbandry factors, such as time spent outside or disinfectant use, were compared using Wilcoxon rank sum tests on all four breeding parameters. To investigate a potential influence of adult sex ratio on breeding success, the deviations from an even sex ratio for each zoo that sexes all its birds ($n = 10$, excluding Wuppertal and Vienna) were calculated. The formula for the deviation from an even sex ratio was derived from Wilson and Hardy's (2002) equation, expressing sex ratio as the proportion of the population made up by males. The value of 0.5 was subtracted from this proportion to get the deviation:

$$\text{Deviation from even sex ratio} = \frac{\# \text{males}}{\# \text{males} + \# \text{females}} - 0.5$$

A linear model analysis was run to examine the potential influence of density on the deviation from an even sex ratio, followed by a linear model to determine whether there was a relationship between the deviation from an even sex ratio and mean egg productivity.

Basel Zoo matrix model

Since 1972, the king penguins at Basel Zoo have been held in the same enclosure and we have therefore used this as the starting point for our matrix model. Annual censuses of the Basel Zoo population taken at the end of each year from 1972 to 2011 (see Supplementary Figures S1, S2) were used to parameterise stage structured matrix models (e.g. Caswell 2001). Stages referred to developmental status as follows: chick (year 1), subadult (years 2–3), and adult (starting year 4). Only females were modelled in this analysis and reproduction was assigned solely to adult females.

The number of chicks produced by adult females (P_{13}) was determined as the ratio of chicks at $t+1$ divided by adult females at t (column c_{t+1} divided by f , Supplementary Table S2). The probability of chicks becoming subadults (P_{21}) was determined as the ratio of chicks becoming subadults ($c \rightarrow s$) divided by the number of chicks (c_{t+1} , from the previous year). The probability

of subadults becoming adult females (P_{32}) was determined by dividing the number of subadults becoming females ($s \rightarrow f$) in a given year by the number of subadults (s). Finally, the probabilities of remaining in a given stage (P_{22} and P_{33}) were determined by the ratio of the number of individuals in that stage at $t+1$ divided by that number at t (i.e. s_{t+1}/s and f_{t+1}/f , respectively). Individuals that would eventually be transferred to other zoos were treated as dead (i.e. leaving the Basel Zoo population) but their fate was taken into account up until and including the year they were transferred. In addition, unknown sexed individuals, as well as eggs and chicks of unknown parents, were not accounted for in this analysis, as these occurred only rarely.

The population's deterministic growth rate at stable stage distribution, λ , was found as the dominant eigenvalue of the matrices and the right eigenvector produced the stable stage distribution. The elasticities of matrix elements are the relative changes in λ when small changes are made to a single matrix element (De Kroon et al. 2000). Residence time (R_{ij}) refers to the time an individual spends in each stage and was found as follows

$$R_{ij} = \frac{1}{1 - S_{ij}}$$

where S_{ij} are the probabilities of staying in a given stage (i.e. the diagonal element of a projection matrix).

Stochastic growth rates (λ_s) were either based on Tuljapurkar's approximation (1982) or using the R-package 'popbio' (Stubben and Milligan 2007) with 10,000 stochastic simulations of environmental stochasticity using matrix sampling.

Using demographic stochasticity as well as environmental stochasticity, the probability of falling below a threshold population size (probability of decline) was estimated by counting the number of stochastically simulated populations (over 25 years) falling below that threshold and dividing it by the total number of simulations (100). Demographic stochasticity was simulated by drawing random numbers from a binomial distribution for survival and from Poisson distributions for the number of individuals (e.g. Akçakaya et al. 1999). Environmental stochasticity was simulated with matrix sampling. At each iteration, one of the yearly matrices was selected randomly with equal probability. Matrix sampling may be considered more appropriate than element sampling, because it preserves potential correlations of demographic parameters (e.g. trade-offs between survival and reproduction; Caswell 2001). Confidence intervals of probability of decline were estimated by replicating the stochastic simulations 100 times and taking the 2.5 percentile on either side of the replicates. Thus, the total number of stochastic simulations was actually 10,000 (100 simulations multiplied by 100).

Probability of decline was estimated using matrices constructed from years with large (more than 15 individuals including males, females, subadults and chicks), medium (10 to 15) and small colonies (less than 10). These thresholds between colony sizes were chosen to give roughly equal numbers of years with small and medium sized colonies. In addition, matrices with equal, male-biased and female-biased adult sex ratios (ratios of 0.5, more than 0.5 and less than 0.5, respectively), were used to estimate probability of decline. All probability of decline curves were estimated using initial stage distributions based on end of year numbers from 2012 and are as follows: two chicks, one subadult, and six adult females. This gives an initial distribution of 0.222, 0.111, and 0.667, respectively.

Results

Husbandry practices and breeding success among zoos

Across the 12 zoos examined, mean egg productivity of king penguins over the five years studied ranged from 0.14 to 0.50 eggs

Table 1. Breeding success parameters of king penguins in the 12 zoos examined.

Zoo	Egg productivity	Hatching success	Chick survival	Chick productivity
Basel ^{1,2,3,4,5,6,9}	0.45	0.45	0.93	0.17
Antwerp ^{1,2,8,10}	0.14	0.20	0	0
Munich ^{1,2,6,8,9}	0.15	0.33	0	0
Zurich ^{2,3,4,5,7,9}	0.38	0.22	0.17	0.029
Wuppertal ⁹	0.33	0.13	0.33	0.012
Vienna ^{1,2,6,9,10}	0.28	0.067	1	0.022
Rotterdam ^{6,9,10}	0.23	0.34	0.20	0.0087
Cincinnati ^{1,2,3,4,5,6,7,8}	0.39	0.46	0.67	0.073
Omaha ^{1,2,6,7,8,10}	0.50	0.12	0.56	0.038
Odense ^{1,2,6,8,10}	0.32	0.33	0.40	0.034
Moody ^{1,2,4,8,10}	0.47	0.099	1	0.043
Edinburgh ^{1,2,3,4,5,6,9,10}	0.14	0.38	0.50	0.020

All values are means across five years. Egg productivity is defined as the number of eggs laid per adult. Hatching success and chick survival are the proportion of eggs hatched per eggs laid and chicks fledged per chicks hatched, respectively. Chick productivity refers to the number of chicks fledged per adult. ¹Egg was incubated by parents (incubated artificially), ²Chick was raised by parents (raised by hand), ³Penguins had access to outside at least part of the year (never outside), ⁴Interactive show where penguins are exposed to visitors takes place (no interactive show), ⁵Penguins perform scheduled walks (no walks), ⁶All penguins swim regularly (some or all never swim), ⁷Use of fungicide in enclosure (no use of fungicide), ⁸Use of disinfectant in enclosure (no use of disinfectant), ⁹Enclosure includes natural light (no natural light), ¹⁰Water in pool is saltwater (freshwater only). If a superscript is missing, the case in parentheses holds true.

laid per adult individual. Mean hatching success (number of chicks hatched per number of eggs laid) had a minimum of 0.067 and a maximum of 0.46. Mean chick survival (number of chicks that fledged per number of chicks hatched) ranged from 0 to 1 and mean chick productivity from a yearly 0 to 0.17 chicks fledged per adult individual (Table 1).

Among zoos, mean hatching success, mean chick productivity and mean chick survival were found to be unrelated ($P > 0.1$; detailed statistics in Supplementary Table S3) to king penguin density (number of king penguins per m^2 of land) or total density (number of birds, including other species, per m^2 of land). However, mean egg productivity increased with increasing king penguin density (Fig. 1 and Supplementary Fig. S3), and with total density the relationship was marginally significant (Fig. 2). Wilcoxon rank sum tests showed no difference ($P > 0.1$) in mean hatching success between eggs incubated by a parent and eggs incubated by an incubator, and mean chick survival did not differ between chicks

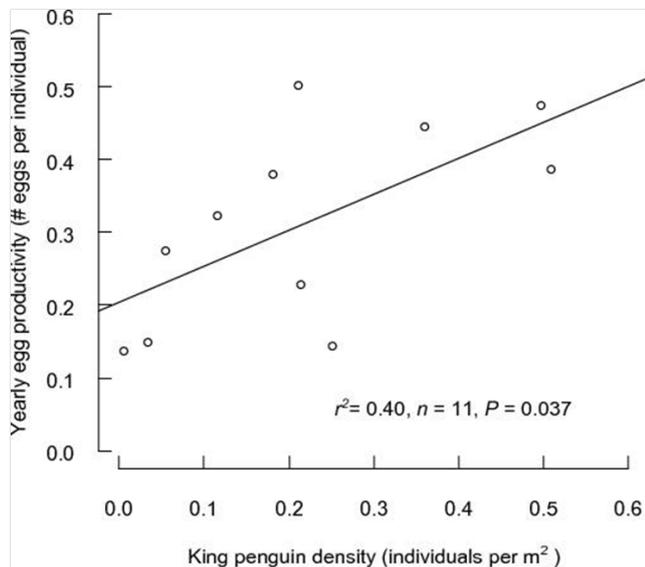


Figure 1. Relationship ($F_{1,9} = 6.0$, $r^2 = 0.40$, $P = 0.037$) between mean egg productivity and king penguin density in 11 zoos.

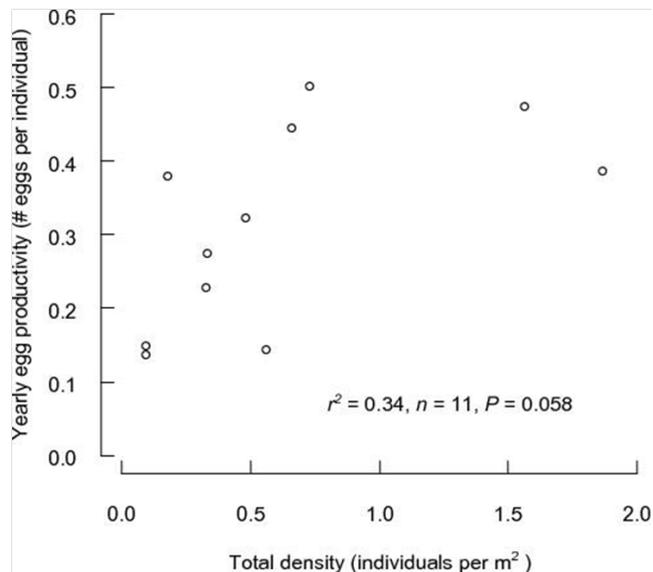


Figure 2. Relationship ($F_{1,9} = 4.7$, $r^2 = 0.34$, $P = 0.058$) between mean egg productivity of king penguins and total density in 11 zoos.

raised by their parent(s) and chicks raised by hand (Supplementary Table S3). In addition, none of the breeding success parameters differed according to the following distinctions among zoos (for all, $P > 0.1$): regular swimming versus no swimming, natural light versus only artificial light, use of fungicide in the enclosure versus no fungicide, use of disinfectant versus no disinfectant, and enclosures containing saltwater versus those with only freshwater (Table 1, Supplementary Table S3). Also, no differences in mean egg productivity, mean hatching success or mean chick survival were found between zoos with interactive shows and those without ($P > 0.1$). Interestingly though, mean chick productivity was marginally significantly greater in zoos with interactive shows ($n = 5$) than in those without interactive shows ($n = 7$) ($W = 30$, $P = 0.051$). Furthermore, zoos that performed outside walks ($n = 4$) with their king penguin group at least part of the year (led by a keeper, with zoo visitors watching and following) showed greater mean hatching success than those zoos that did no such walks ($n = 8$) ($W = 29$, $P = 0.028$).

All zoo populations were more or less male-biased over the five years studied, though some maintained values very close to an even sex ratio (Fig. 3). Mean egg productivity decreased with increasing deviation from an even sex ratio (Fig. 4, Supplementary Table S3), which did not originate from a relationship between density and deviation from an even sex ratio ($F_{1,8} = 2.2$, $r^2 = 0.22$, $n = 10$, $P = 0.17$). Further, a marginally significant relationship was found between the deviation from an even sex ratio and mean population size (Supplementary Fig. S4).

Basel Zoo matrix model

The mean matrix of Basel Zoo's king penguin population, averaged over 39 annual transitions (Supplementary Table S2), is shown in Table 2. The deterministic growth rate (λ) of this mean matrix was 0.981, with a simulated stochastic lambda of 0.964 (0.956–0.971, 95% CI, based on 10,000 simulations). The stable stage distribution was found to be 0.207 chicks, 0.128 subadults and 0.665 adult females, for which the average residence times were 1.00, 1.38

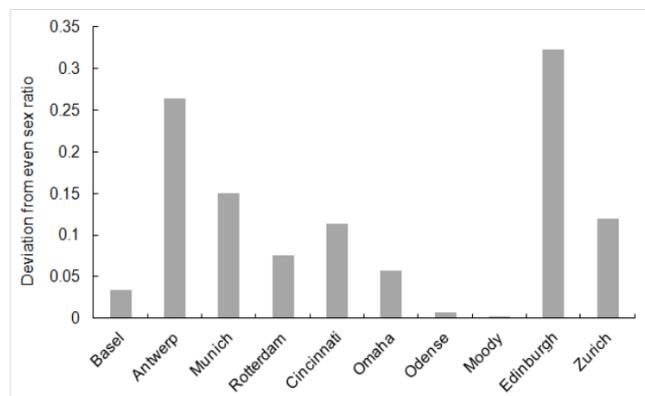


Figure 3. Deviations from an even sex ratio in king penguins at the 10 zoos examined for the years 2007–2011. Positive values indicate male-biased sex ratios.

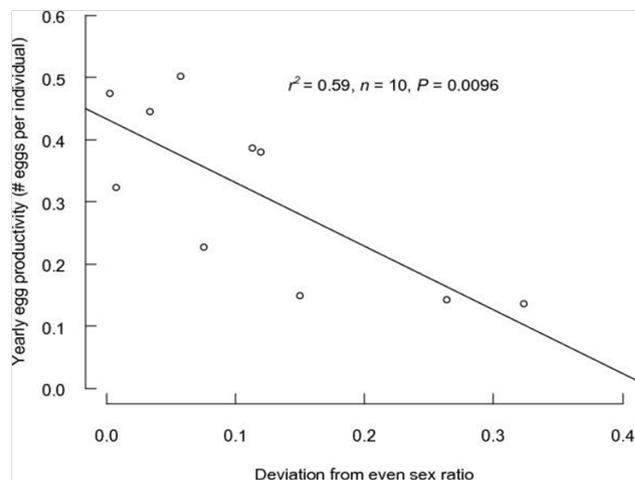


Figure 4. Relationship ($F_{1,8} = 11$, $r^2 = 0.59$, $P = 0.0096$) between mean egg productivity and the deviation from an even sex ratio in king penguins at 10 zoos.

Table 2. Average transition matrix over 39 annual transitions of the king penguin colony at Basel Zoo.

	Chicks (c)	Subadult (s)	Adult female (f)
Chicks (c)	0.00	0.00	0.30
Subadult (s)	0.44	0.28	0.00
Adult female (f)	0.00	0.14	0.95

and 21.5, respectively. Approximate elasticities were highest in adult female survival and lowest in subadults remaining subadults (Table 3).

Annual transitions were partitioned based on colony size at the end of the year. There were six years with a colony size greater than 15 individuals, for which the simulated stochastic λ of the mean matrix was significantly less than 1 (Table 4). There were 18 years with a colony size between 10 and 15, for which the simulated stochastic λ was significantly greater than 1. Finally, colony size was less than 10 in 15 years and the stochastic λ of the average matrix across these years was significantly less than 1. The first eight years in the analysis (1972–1979) showed no change or reproduction in the population (Supplementary Table S2) and we assumed this might be due to the colony adjusting to their new enclosure. We thus calculated the above annual transitions again without this initial period (Supplementary Table S4) and with varied colony size categories as a sensitivity analysis. Even with varying colony size categories, the stochastic λ of large colonies remained significantly less than 1 and that of medium sized colonies significantly greater than 1. The results for small colonies were split between those with a stochastic λ significantly smaller than 1 and those not significantly different from 1, depending on how colony size was categorised.

Probability of decline curves showed a higher risk of decline for years with large or small colonies compared to all years pooled (Fig. 5). The probability of decline was lowest if only years with medium sized colonies were used for the stochastic simulations. Whereas the probability of decline below five individuals was clearly larger than 50% for years with small or large colonies, it was roughly 50% for years with medium sized colonies.

The growth rate of matrices with equal adult sex ratios ($n = 4$) was 1, whereas male-biased ($n = 25$) and female-biased matrices ($n = 10$) displayed simulated stochastic λ 's that were significantly

Table 3. Approximate elasticities of the average transition matrix for the king penguin colony at Basel Zoo.

	Chicks (c)	Subadult (s)	Adult female (f)
Chicks (c)	0.000	0.000	0.026
Subadult (s)	0.026	0.010	0.000
Adult female (f)	0.000	0.026	0.912

less than 1 (Table 4). The results of the second analysis without the first eight years showed similar results (Supplementary Table S4). Male-biased populations displayed the highest risk of decline, whereas populations with an equal sex ratio have a zero percent chance of falling below a threshold of five individuals (Fig. 6). If the range of equal sex ratios was extended to include 0.45–0.55, the differences in probability of decline between male (> 0.55) and female-biased (< 0.45) sex ratios became even larger (Supplementary Fig. S5).

Egg productivity first increased with colony size up to 12 individuals, then decreased with further increasing colony size in a non-linear, parabolic fashion (Fig. 7). Chick productivity increased linearly with colony size (Fig. 8).

Discussion

Density

Among zoos, a positive relationship was found between mean egg productivity and king penguin density (Fig. 1). Replacing king penguin density with total density of birds maintained within the enclosure gave a marginally significant relationship. Also, the analysis of the Basel Zoo population showed a curved relationship between egg productivity and colony size, with egg productivity first increasing with colony size up to 12 individuals, then decreasing as colony size increased further (Fig. 7). Chick productivity increased linearly with colony size in the Basel population (Fig. 8). Furthermore, years with a medium colony size of 10 to 15 king penguins (which corresponds to 0.25 to 0.38 individuals per m^2) had a growth rate larger than 1, indicating a growing population, while average matrices of years with small or large colonies had growth rates of less than 1. Medium sized colonies also displayed a lower probability of decline than years with a small (fewer than 10 king penguins) or large (more than

Table 4. Growth rates of the king penguin colony at Basel Zoo for average matrix over 39 annual transitions and average matrices of years with different colony sizes and adult sex ratios. n = number of matrices, λ = growth rate, 95% confidence interval based on 10,000 simulations.

	n	Deterministic λ	Stochastic approximate λ	Stochastic simulated λ	95% confidence interval
Mean matrix	39	0.981	0.972	0.964	0.956 – 0.971
Colony size > 15	6	0.913	0.910	0.905	0.900 – 0.910
Colony size 10 to 15	18	1.016	1.012	1.008	1.003 – 1.013
Colony size < 10	15	0.969	0.955	0.942	0.932 – 0.951
Equal sex ratios	4	1.000	1.000	1.000	0.996 – 1.004
Male biased	25	0.967	0.955	0.947	0.938 – 0.955
Female biased	10	0.980	0.976	0.975	0.970 – 0.979

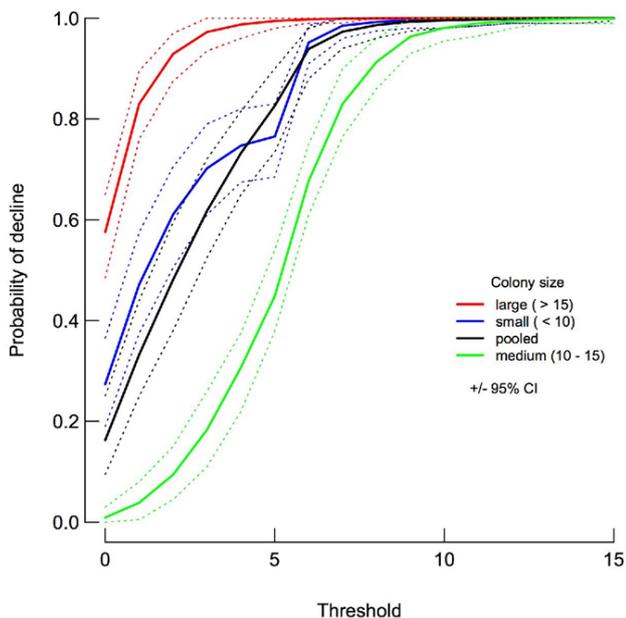


Figure 5. Risk of decline for populations simulated over 25 years with demographic and environmental stochasticity, based on years with large (red line), medium (green) and small (blue) colonies. The black line represents all years pooled. The y-axis gives the probability that the population size will fall below a certain threshold on the x-axis. Dotted lines give approximate 95% confidence intervals constructed by replicating sets of 100 stochastic simulations 100 times.

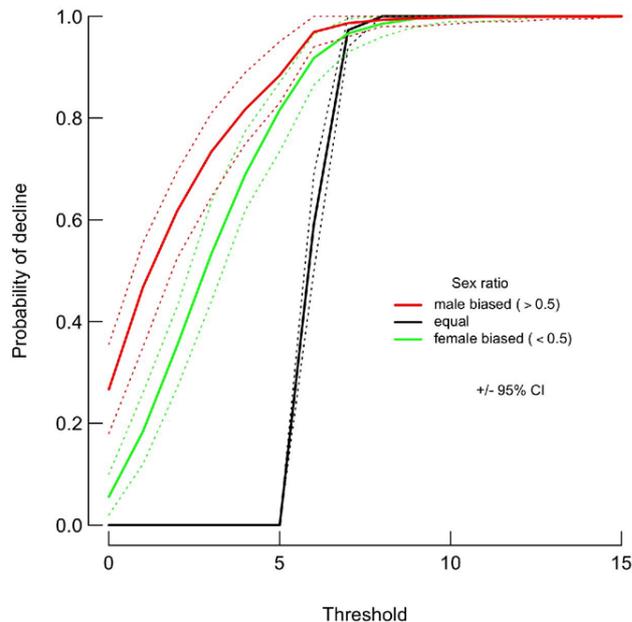


Figure 6. Risk of decline for populations simulated over 25 years with demographic and environmental stochasticity, based on populations with equal (black line), male-biased (red), and female-biased (green) sex ratios. The y-axis gives the probability that the population size will fall below a certain threshold on the x-axis. Dotted lines give approximate 95% confidence intervals constructed by replicating sets of 100 stochastic simulations 100 times.

15) colony size.

Density dependence has previously been linked to colonial bird population sizes. Kim et al. (2009) found that blue-footed boobies at high densities move to lower density patches, while at lower density they dispersed to higher density patches. A colony of Magellanic penguins showed highest breeding success in medium nest-density areas and low success in areas of very low and very high nest densities (Scolaro 1990). King penguins on

subantarctic islands gather in extremely dense colonies to breed, with only approximately 0.5 m² of territory for each pair (Barra, 1976; Weimerskirch et al. 1992). Within such large colonies, positive density dependence has been observed in respect to population growth rate up until a certain carrying capacity, above which population growth rates decreased (Delord et al. 2004). In extremely small populations, as in zoo populations of king penguins, population growth rate is frequently limited at low

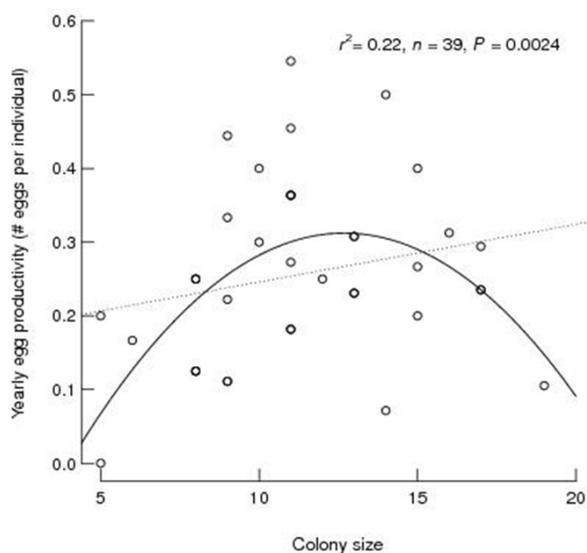


Figure 7. Relationship between yearly egg productivity and colony size (all king penguins including males, females, subadults, and chicks) at Basel Zoo over 39 years. The curved line represents a non-linear fit ($t_{36} = -3.3, r^2 = 0.22, P_{\text{non linearity}} = 0.0024$). The dotted line represents a linear fit that is not significant ($t_{37} = 1.4, r^2 = 0.024, P = 0.17$).

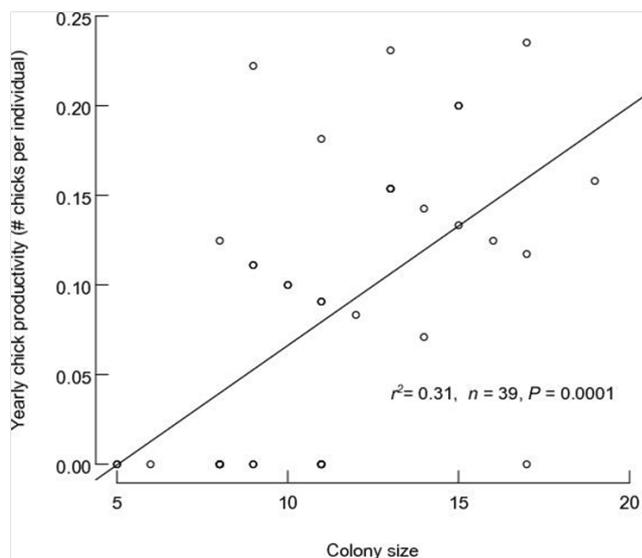


Figure 8. Relationship between yearly chick productivity and colony size (all king penguins including males, females, subadults, and chicks) at Basel Zoo over 39 years. The straight line represents a linear fit ($t_{37} = 4.3, r^2 = 0.31, P = 0.0001$).

densities, which can be explained by the Allee effect (Allee et al. 1949; Stephens and Sutherland 1999). Møller and Legendre (2001) suggested that a reduction in choice of suitable mates could be responsible for decreases in reproductive behaviour and success in small populations of animals exposed to sexual selection. This could also be a factor in small populations of king penguins, as the size of colourful ear patches seems to be sexually selected for in these birds (Dobson et al. 2011). Additionally, the lack of acoustic enrichment may play a role in decreased breeding behaviour in populations with low densities. Studies on wild populations of royal penguins, as well as on captive populations of Northern bald ibis, have shown that reproductive behaviour increases when recordings of breeding vocalisations are played (Waas et al. 2000; Clark et al. 2012). Further research examining the effect of density on breeding success would surely provide insights. However, based on the results of this study, most king penguin holders should opt for higher densities within their king penguin enclosures, possibly between 0.25 and 0.38 individuals per m² (corresponding to a population size in Basel that displayed growth rates larger than 1).

Interactive shows

Curiously, mean hatching success was greater in zoos performing outside walks with their king penguins than in those that did not. Furthermore, mean chick productivity was marginally higher in zoos with interactive shows than in those without. Interactive shows could involve, for example, paid encounters with penguins or outside walks with visitors looking on – any activity that either brought zoo visitors to the penguins or vice versa. Thus, a limited amount of human interaction, outside that with keepers, may be enriching for zoo animals, as has previously been suggested by Morris (1964). Actual research on this, however, is limited and almost exclusively focused on primates (Hosey and Druck 1987; Choo et al. 2011). Another explanation might be a habituation effect. Greater rheas in a Brazilian zoo showed habituation to visitor presence and it was suggested that these animals were less stressed in their captive environment due to this habituation (de Azevedo et al. 2012). A study on captive ground squirrels has shown animals exposed to visitors to be calmer and display more natural behaviours in the presence of humans, including zoo staff, than those never exposed to visitors (Górecki et al. 2012). Similarly, the higher hatching success and chick productivity in king penguin zoo populations with increased exposure to visitors could result from more natural parenting behaviour in the presence of humans, including keepers and veterinarians.

Sex ratios

The adult sex ratio seems to play a vital role in the breeding success of king penguins in zoos. Among the zoos studied, mean egg productivity decreased with increasing deviation from an even sex ratio (Fig. 4). Also, within Basel's population, years of equal adult sex ratios had a significantly higher growth rate than male-biased and female-biased years. Probability of decline curves further demonstrated the highest risk of extinction for male-biased populations, whereas populations with an equal sex ratio had a zero percent chance of falling below a threshold of five individuals. It should be noted that the sample size of four years with equal sex ratios is relatively small, and that in all four years it could be a coincidence that no adult females died. But if the range of equal sex ratios was extended to include 0.45–0.55, probability of decline curves still displayed the highest risk of extinction for male-biased populations, followed by female-biased and equal sex ratio populations. These results are critical, as the majority of zoo populations considered in this study were considerably male-biased. Similarly, the overall population in the European Studbook is extremely skewed towards males, with 121 adult males and only

80 adult females at the end of 2008 (Elliot and Talbot 2009). Yet it remains unclear whether this skew is due to a bias in hatching sex ratios or higher female than male mortality.

Studies of populations of king penguins on subantarctic islands have found similar male-biased sex ratios in displaying adults (Olsson and van der Jeugd 2002; Pincemy et al. 2010). Olsson and van der Jeugd (2002) also discovered that female survival was significantly lower than male survival following a year of food stress, though they were careful not to make any generalised assumptions about sex-biased mortality rates.

An additional analysis showed that larger populations exhibited more equal sex ratios and this in turn may increase egg productivity. This raises the question of whether it is really density or the more equal sex ratio, or both, that is responsible for increased egg productivity. Indeed, if both density and deviation from an equal sex ratio were fitted as independent and egg productivity as the dependent variable, only the deviation from an even sex ratio remained significant, yet a regression analysis on density and deviation from an even sex ratio revealed no significant relationship. Nevertheless, based on the results found in this study, zoological institutions holding king penguins should focus on maintaining their populations close to an even adult sex ratio. Also, for those institutions which do not know the sex of their king penguins, effort should be put into determining the sex of all adults held, so that management decisions can be made accordingly to increase breeding success.

Basel Zoo matrix model

The stage-based matrix analysis of the Basel Zoo population from 1972 to 2011 was insightful in that it highlighted how well this zoo manages its king penguins, as shown by the intrinsic growth rate, λ , being actively maintained close to a stable value of 1. The zoo has also kept its population very close to an even adult sex ratio over the last 10 years. Average residence times showed subadults remained in that stage an average of 1.38 years, which is due to most king penguins moving to other zoos leaving while at this stage. Adult females displayed the longest average residence time, at 21.5 years, and this stage also had the highest elasticity value. Hence, small changes in the survival of adult females will have large effects on the population growth rate, which should be considered when making management decisions.

Conclusions

1. Higher king penguin density within enclosures was positively related to egg productivity among the zoos studied. At Basel Zoo, yearly egg productivity increased with colony size up to 12 individuals, then decreased with colony size. Yearly chick productivity was positively related to colony size.
2. Years with densities between 0.25 and 0.38 individuals per m² displayed larger growth rates than years with higher or lower densities at Basel Zoo. The probability of colony decline was also lowest at these medium densities.
3. All zoos studied exhibited male-biased sex ratios. Increasing deviation from an even adult sex ratio was related to decreased egg productivity. In the Basel population, years with even sex ratios showed the highest growth rate and the lowest probability of decline.
4. Zoos with increased visitor interaction displayed higher hatching success and chick productivity that was marginally significantly greater than those without outside walks or other interactive shows.

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