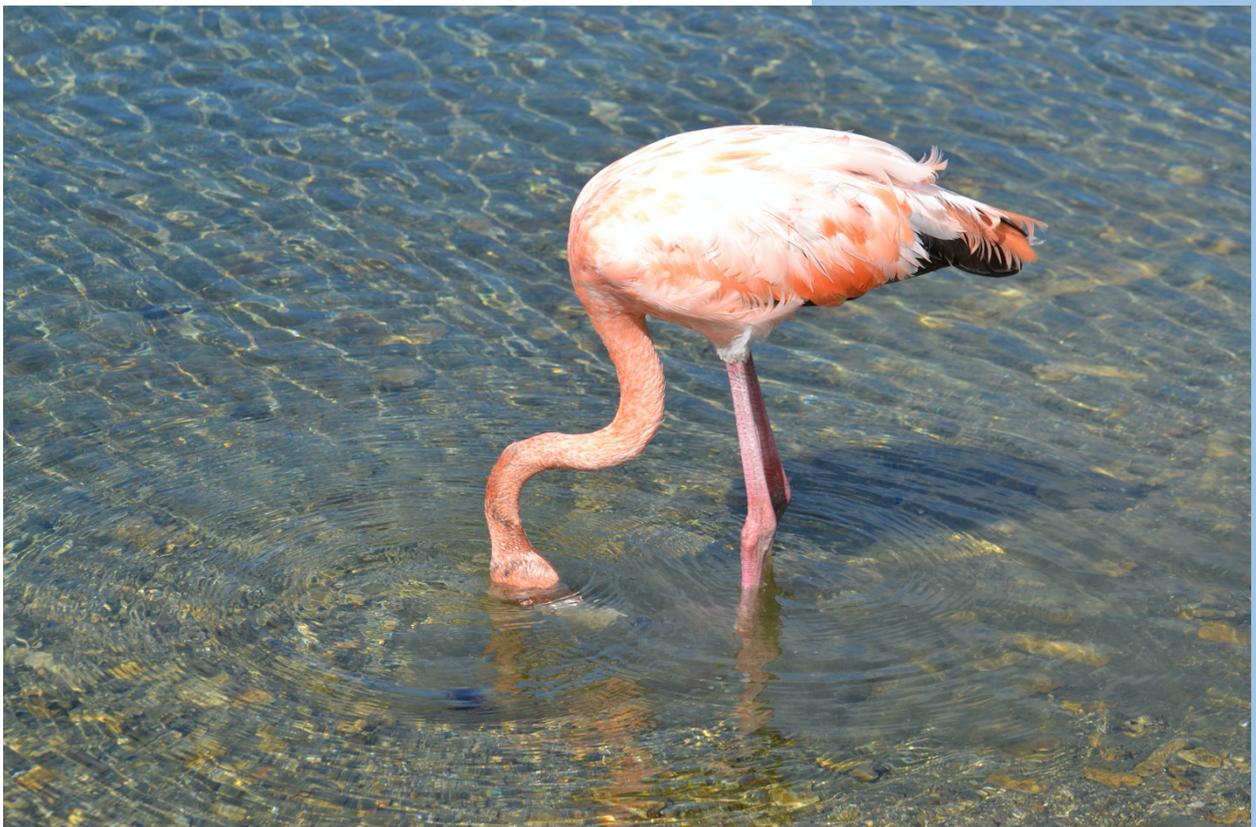


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Abstract

Since 2018, increasing number of dead juvenile flamingos were found on Bonaire. This study aims to determine what reproduction rate is required to keep the population stable or increasing, by constructing and analysing a population model. However, a literature search for estimates of the vital rates of the Caribbean flamingo shows that these are largely unknown or have a high degree of uncertainty. Clutch size is estimated to be 1, breeding success is estimated around 40%, juvenile and adult survival is estimated to be high, age of first reproduction is estimated to be 3 and the breeding chance is unknown. Usage of data from a ringing project in Yucatan, Mexico, could improve the estimates. A general ‘flamingo’ population model shows that annual population dynamics of flamingos is mainly determined by adult survival. Incidental years with low chick survival are therefore unlikely to have a large effect on a population. Thus far, the reason for the increasing number of dead juvenile flamingos found on Bonaire remains unknown. Additional information about the population in Venezuela is necessary for understanding the population dynamics on Bonaire, since flamingos frequently fly from and to the mainland.

Introduction

Flamingos are large, long-lived birds that generally breed in large colonies in lagoons, salt water lakes and ponds (Allen 1956, Zweers et al. 1995). Successful breeding depends on colonies being inaccessible to terrestrial predators (Cezilly et al. 1996). Predation risk in these lagoons and lakes is generally low (Rooth 1965). However, human disturbance can decrease breeding success (Gerharts & Voous 1966).

The Caribbean flamingo (*Phoenicopterus ruber*) can be found in the Middle American region. On Bonaire and in Venezuela the population is estimated at more than 30,000 individuals (Espinoza et al. 2000). Bonaire hosts one of the four major breeding grounds for these flamingos (de Boer 1979, Mawhinney 2008). Predation risk in the salt pans is low but (continued) human disturbance by joggers, tourists or motor vehicles might impact flamingo behaviour (Galicia & Baldassarre 1997, Yosef 2000), and disturbance of the colonies can result in a loss of eggs and chicks (Gerharts & Voous 1966; Baldassarre & Arengo 2000). Caribbean flamingos show great resilience to short-term disturbances such as natural disasters. Flooding of the breeding areas due to periods of heavy rain severely impacted nest success and chick survival in 1966 (Gerharts and Voous 1966) and only a small number of eggs and chicks survived the flood. Yet, flamingos started building nests and breeding soon after the water level dropped (Gerharts & Voous 1966).

In 2018 and 2019, Bonaire residents found a large number of stressed, lost or dead flamingo chicks and brought them to the Wild Bird Rehab centre (Engel & Johnson 2019). There the flamingos are cared for, and released near the resident colony when healthy. On the 12th of May 2019, the Wild Bird Rehab reported that roughly 360 birds were brought in over 8 weeks. The chicks were reported to be undernourished. The same thing had occurred in 2018, although the numbers were not as high as in 2019. Both years had successful breeding and no apparent reasons for this increase in incidents with the flamingo chicks were found (Engel & Johnson 2019).

This study aims to model the population dynamics of the flamingos on Bonaire to understand the impact of juvenile mortality on the survival of this population. The necessary estimates for vital rates will be gathered from literature and then used to model the population dynamics. With this model, the impact of juvenile mortality on the population growth will be assessed.

Materials and methods

Literature search

The search engines Web of Science and Google Scholar were used to find relevant literature for the vital rates (i.e. clutch size, breeding success, juvenile survival, adult survival, minimum age of reproduction and breeding chance) of the Caribbean flamingo. The searches were conducted in English with *Phoenicopterus ruber*, vital rates, population size, survival, ringing, clutch size, reproduction and breeding as keywords and in Spanish with *Phoenicopterus ruber* and anillados (i.e. ringed) as keywords. At first, only the scientific name of the species was used, and in later searches, one of the other keywords was added to obtain more specific results. The results were selected based on title and abstract. For potentially relevant papers, the whole paper was scanned and read Spanish reports were translated with deepL Translator to English. When estimates for a vital rate for the Caribbean flamingo could not be found, we searched (using the same key words, but only the genus name) for estimates of these vital rates for other flamingo species, which have roughly similar life histories.

Population model

The vital rates of the Caribbean flamingo were used to create a Leslie (i.e. age-structured) population model. When the rates could not be found for the Caribbean flamingo, the vital rates of the greater flamingo (*Phoenicopterus roseus*) were used as a proxy. The lambda (projected population growth rate) and the elasticity of the matrix model were calculated using the IPMpack package (Metcalf et al. 2013) in R. Additionally, the effect of the fecundity on the population growth was calculated.

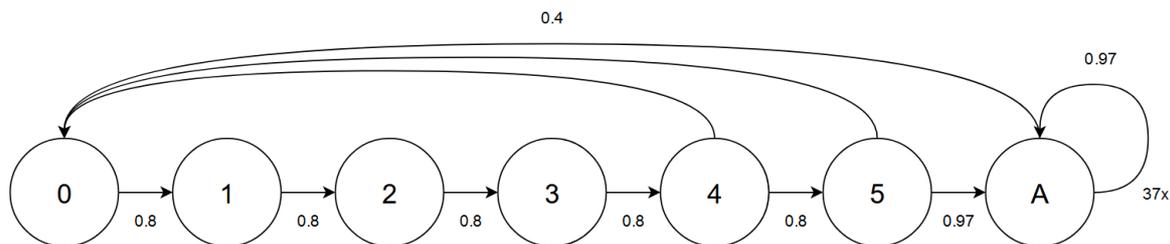


Figure 1. Modelled life cycle of the Caribbean flamingo population. The circles represent the ages 1 to 5 and adult, the arrows indicate the contributions to the age classes. Juvenile survival is 0.8, adult survival is 0.97 until the age of 42. Fecundity is estimated to be 0.4 and age of first reproduction is set at 4. See also Table 1. This life cycle results in a growth rate of 1.10.

Results

Quantitative information about the vital rates of the Caribbean flamingo was limited in the searched literature. Below we present our findings for each of the vital rates. The found rates for the Caribbean flamingo are discussed first, and when necessary the vital rates of other flamingo species are discussed as well. Additionally, potential additional sources (which were currently not accessible) for the vital rates of the Caribbean flamingo are mentioned.

Clutch size

The normal clutch size is one egg (Pickering 1992). Rooth (1965) found two nests with two eggs and two nests containing both a one-to-two-day-old hatchling and an egg. The number of checked nests is not mentioned, however, and it remains unclear how frequently clutch size of 2 eggs occurs. For this study we assume a clutch size of one.

Breeding success

Over slightly more than one year (1959-1960) Rooth (1965) observed the breeding success of 2458 breeding pairs. In this period 1817 young fledged the nest, resulting in an average breeding success of 73% for the breeding grounds on Bonaire. This survival from egg to juvenile varied from 64 to 83% for various spots on Bonaire. Most unsuccessful breeding attempts resulted in unhatched eggs (21-27%), only few resulted in dead hatchlings (less than 6%) (Rooth 1965).

In Yucatan, Mexico, the breeding success varied between 0% and 94.6% between 1999 and 2007 based on count estimates. The average breeding success of 83428 pairs was 46.6% (SD = 45.2%) (von Bertrab & Contreras 2010). In captivity at the Wildfowl and Wetlands Trust Centre in Slimbridge, Caribbean flamingos had 16 successful breeding seasons between 1968 and 1990. On average 46% (SD = 18.3) of the eggs hatched successfully over this period. The percentage of independent chicks reared from laid eggs ranged from 22% to 88% with an average of 38%. (Pickering 1992). Re-nesting can happen after natural disasters such as floods, however, it is not known how often re-nesting happens in the wild. In captivity, in Slimbridge, 4 out of the respectively 31 and 27 eggs were lost in 1989 and 1990. In both years re-laying was attempted once (Pickering 1992).

STINAPA has been counting the number of juveniles, adults and breeding pairs on Bonaire every month since 1981. To increase the accuracy of the breeding success estimates it is advisable to inspect the breeding grounds for remaining eggs and dead chicks when those counts take place.

Juvenile survival

Rooth (1965) estimated that juvenile survival is very high, although he does not give an estimate. He only found a few dead juvenile birds during his yearlong stay on Bonaire. No other estimates of the juvenile survival were found.

Additional data could be obtained from a ringing project in Mexico. However, we were unable to access these data during our study. Ringing data from the “Programa Integral de Conservación del Flamenco” which is led by the Comisión Nacional de Áreas Protegidas and the Organización Niños y Crías A. C. (Plasencia-Vázquez et al. 2017) might be useful to estimate juvenile survival. Plasencia-Vázquez et al. (2017) used resightings from 2010-2015 of flamingos ringed between 1996 to 2014. Although the total number of resightings is not mentioned in the article, table 1 and 2 give an overview of the data. The resightings (in their Table 2) add up to 16,405. The number of individuals differ between the tables. In their Table 1, which gives an overview of all the areas, these add up to 5,643 individuals and in their Table 2, which gives an overview of the individuals and resightings per age, the individuals add up to 4,803. Whether the ringing project continued after 2014 remains unclear but it is likely because the organisation still exists and still works on flamingo projects.

For greater flamingos (*Phoenicopterus roseus*) in the Camargue (southern France), juvenile survival is estimated to be $81\% \pm 3.3\%$ during normal winters when these greater flamingos stay in France (Sanz-Aguilar et al. 2012). Because of differences in winter conditions between Bonaire and France, juvenile survival might be even higher for the Caribbean flamingo.

Adult survival

For adult survival no estimates were found either. Again, these could probably be estimated using the ring data gathered in Yucatan, Mexico (Ferrer-Sánchez et al. 2017, Plasencia-Vázquez et al. 2017).

Ringed greater flamingos in the Camargue, France, were estimated to have an annual local survival of 94.3% (SD = 0.003) between 1977 and 2010 (Sanz-Aguilar et al. 2012). In 1984-1985, due to a severe cold spell, survival fell to 76% (Cezilly et al. 1996). Pradel et al. (2012) estimated the survival of greater flamingos in the Camargue at 0.97 ± 0.001 in normal years and 0.84 ± 0.02 during the cold spell in 1984.

To better estimate juvenile and adult survival of the population on Bonaire, ringing, marking and/or tracking birds should be started. However, capturing birds without causing injuries and/or severely stressing them has proven to be difficult.

Age of first reproduction

The age at which Caribbean flamingo start breeding is unknown for wild populations. Ringing or marking and then resighting individuals for multiple years is necessary to determine this age of first reproduction. In captivity, three-year-old flamingos were reproducing according to Pickering et al. (1992), but they do not mention to which flamingo species they are referring. For ringed greater flamingos (*Phoenicopterus roseus*) the age of first reproduction is approximately age 3. After breeding for the first time, breeding was not attempted the following year until the age of 6 by the 14716 ringed greater flamingos in the Camargue (Pradel et al. 1997, 2012).

Breeding chance

Due to the flamingos flying back and forth between Venezuela and Bonaire the population size is not known, thus the breeding chance cannot easily be calculated from the number of breeding pairs. There is a dataset with monthly counts from 1981 till now (January 2020), which provides the number of breeding pairs on Bonaire (unpublished data from STINAPA). Because birds are not marked, they cannot be tracked individually. Estimates of the total population size and this migration between Venezuela and Bonaire are necessary to calculate an overall breeding chance of the population.

Table 1. The vital rate estimates which were found in literature and used in the model, with references.

Vital rate	Literature estimate	Model estimate	Reference
Clutch size	1 (very rarely 2)	1	Rooth 1965, Pickering 1992
Breeding probability	unknown	60%	
Breeding success	73%, 46%, 38%,	66%	Respectively: Rooth 1965, Pickering 1992, von Bertrab & Contreras 2010
Juvenile survival	81% for <i>P. roseus</i>	80%	Sanz-Aguilar et al. 2012 (<i>P. roseus</i>)
Adult survival	94.3% and 97% for <i>P. roseus</i>	97%	Respectively: Sanz-Aguilar et al. 2012, Pradel et al. 2012 (<i>P. roseus</i>)
Age of first reproduction	Age 3 or 4 with a gap for <i>P. roseus</i>	Age 4 without gap	Pradel et al. 2012 (<i>P. roseus</i>)

Population model

As several important vital rates could not be estimated for the Caribbean flamingos, we used estimates for the Greater flamingo (*P. roseus*) instead. Our population model, constructed with the above-mentioned vital rates (Fig. 1, Table 1), therefore represents a general ‘flamingo’ population, and is mainly used to explore the relative importance of reproduction, juvenile survival and adult survival. This particular matrix model has a projected population growth rate of 1.1. In this model age of first reproduction is set to 4 because consecutive breeding does not occur before the age of 5. Aging is limited as well: in the model no individual can become older than an age of 42 (Fig. 1).

In this population matrix, adult survival has a higher elasticity than fecundity (Fig. 2). Both the survival and fecundity decline with age. A lambda above 1 is reached with fecundity is set to 0.101 or higher, based on these vital rates (Fig. 3).

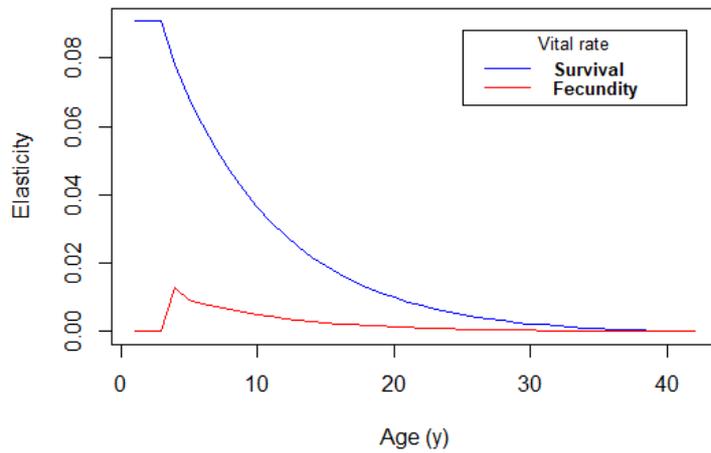


Figure 2. The contribution of survival and fecundity to the population growth rate. The elasticity indicates the relative contribution of the survival and fecundity to the population growth rate. Juvenile survival adds most to the population growth followed by adult survival and fecundity respectively. The elasticity of both survival and fecundity decline with age. Lambda is 1.10 for this population model.

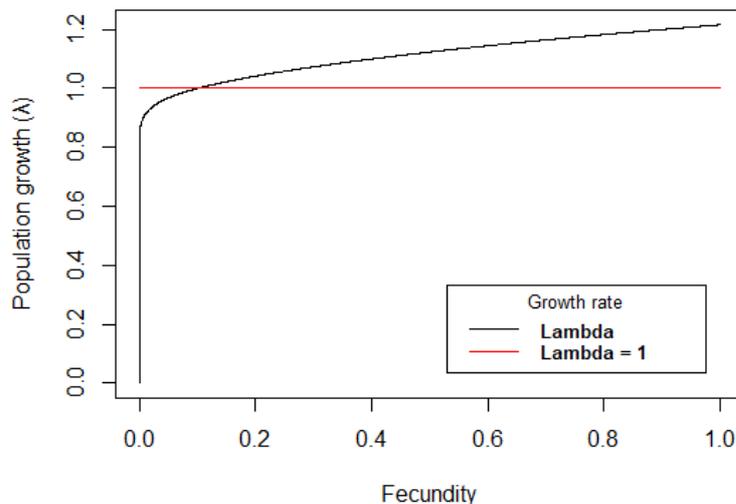


Figure 3. The effect of fecundity on the population growth rate. Population growth of the model is depicted for a fecundity from 0 to 1. Fecundity is defined as the surviving offspring 1 year after the breeding attempt. The minimum growth rate at a fecundity of 0.0001 is 0.797. A lambda of 1 is reached at a fecundity of 0.101. When the fecundity is 1, the lambda is 1.215.

Discussion

Vital rates for the Caribbean flamingo are to a large degree unknown or, if known, uncertain. Most of the estimates reviewed in this report are based on either the 11-month study of flamingos on Bonaire in 1959-1960 by Rooth (1965) or on flamingos held in captivity in Europe (i.e. Pickering 1992, Pickering et al. 1992). However, existing ringing data from Mexico could provide the necessary information to calculate the survival rates and breeding success of the Caribbean flamingo. The Yucatan ringing project has been running for at least 18 years but so far, no mark-recapture analysis or population models have been published using these data. Potentially, these data could vastly improve our understanding of the population dynamics of the Caribbean flamingo.

The population model constructed with these vital rates (Fig. 1) has a lambda of 1.10, which is highly unlikely to be realistic. This high growth rate of 10% per year is likely due to the fact that we used vital rate estimates from a French population of the greater flamingo (*P. roseus*). Again, improved estimates of the vital rates of the Caribbean flamingo are necessary to better estimate the population growth rate. Despite its limitations, this model shows that population growth is mainly dependent on survival and less so on fecundity (Fig. 2). This indicates that the population is probably able to recover quickly from a period of low fecundity. Fecundity is defined in this study as the produced offspring which survived the first year i.e. a successful breeding attempt which results in a one-year-old chick. In this model, fecundity was set to 0.4 while a fecundity of only 0.101 is sufficient to keep the population stable (Fig. 3). Hence, a short-term increase in stressed, injured and dead chick does not necessarily lead to a declining population trend.

Thus far, the reason for the increase in the number of stressed, lost and dead chicks found on Bonaire remains unknown. Several hypotheses could explain this increase. Some are connected to the growing human population on Bonaire. The human population grew from 15,679 inhabitants in 2011 to 20,104 in 2019 (Centraal Bureau voor de Statistiek 2019). It is possible that the increased human population puts increasing disturbance pressure on the flamingo population on Bonaire. It is also possible that there may have always been injured and dead chicks but recently more people found and/or reported them. Additionally, the Wild Bird Rehab centre could have become better known among inhabitants which resulted in more reports. On the other hand, the increase in reports could point to an actual increase of stressed, lost and dead chicks. The flamingo population might be increasing which, while the relative juvenile survival stays constant, results in an absolute increase of injured or dead chicks. However, STINAPA counts show a decline in number of breeding pairs on Bonaire since 1991. Since 2005, breeding pair counts have rarely exceeded 500 pairs during the monthly counts.

We do not know whether there is a net emigration rate of flamingos from Bonaire to nearby Venezuela which could explain the observed decrease. A way to find out or make this more plausible is to study the population development in Venezuela (presently unknown). If the population size and number of breeding pairs Venezuela have increased, this could indicate that the flamingos prefer these sites over the breeding sites on Bonaire, resulting in fewer breeding pairs on Bonaire. However, if the population in Venezuela has been declining too, identifying the bottlenecks and population dynamics of this population becomes even more important.

Additional information gathered during the STINAPA counts can help to identify the cause of the increase in reports. Including stressed, injured and dead chicks and unhatched eggs in the monthly STINAPA counts would help to distinguish between an increase in reports and an increase in lost chicks and unhatched eggs in the future. This information can help to estimate breeding success as well. Combining information about the population size and trend of the Caribbean flamingo in Venezuela and Bonaire would help determine the overall trend of this population. And finally, a way to mark and track individual flamingos is vital for a more comprehensive population model which would lead to a better understanding of the population dynamics. Some of the flamingos released by the Wild Bird Rehab centre were ringed. During the monthly counts, STINAPA should look for these birds and track them as closely as possible because these can provide vital information about the migration pattern of the Caribbean flamingo on Bonaire. However, such ringing data need to be interpreted carefully, as rehabilitating birds often have lower survival and reproduction rates than previously-uninjured birds.

Conclusion

Although the vital rates of the Caribbean flamingo remain uncertain, there are chances to improve these estimates. Using ringing data from Mexico, mark recapture analysis could be performed and vital rates can be estimated. Additionally, combining information about the population on Bonaire with information about the population in Venezuela can increase our understanding of the

population dynamics and size. And finally, with some additions the STINAPA counts could help exclude some of the proposed hypotheses.

However, the constructed model of a general ‘flamingo’ population (i.e. based on estimates from both Caribbean and Greater flamingo populations) shows that the annual population dynamics of flamingos are mainly determined by the survival of adults. While reproduction is of course important in the long run, low reproduction or juvenile survival in some years is unlikely to affect the population much. Nonetheless, we recommend that (unhatched) eggs as well as chicks (healthy, injured, or dead) are counted separately during the monthly censuses.

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