Effective population size in a bottlenecked fur seal population

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ARTICLE INFO

Article history:
Received 1 February 2005
Received in revised form
23 January 2006
Accepted 28 February 2006
Available online 6 June 2006

Keywords:
Effective population size
Arctocephalus australis
Peruvian population
El Niño

ABSTRACT

The census population size (N) is usually the only information available for most threatened species. For evolutionary matters, the effective population size (Ne), not the census number, is a prime concern. Factors such as variation in the sex ratio of breeding individuals, variation of population size in different generations and mating system are important. The South American fur seal, Arctocephalus australis, has been exploited in Peru by humans since ca. 2000 BC and now the original population declined 72%, as a result of low food availability during the severe El Niño in 1997–1998. In this sense A. australis is now classified as in danger of extinction in Peru. We present the first estimate of Ne of the Peruvian population of A. australis that takes into account the effects of mating system and variation in population size caused by the 1997–1998 El Niño. The resulting Ne was 2153 specimens. We believe that the estimated Ne for the Peruvian population is a critical value, because it is significantly lower than the mean minimum viable population for vertebrates (7000 breeding age adults). This estimated Ne is of critical importance because combined with the current El Niño events are reasons of great concern for the survival of the species and should be taken into account in future management plans to ensure the conservation and protection of the species in the Peruvian coast.

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1. Introduction

The populations of most species of seals (family Phocidae) and sea lions (family Otariidae) were substantially reduced by commercial sealers and whalers in the 18th and 19th centuries, and some may have been reduced centuries earlier by coastal aborigines (e.g. Reeves et al., 1992; Wynen et al., 2000). In fact, according to Weber et al. (2004), most species of fur seals were presumed to be extinct by the late 19th century.

The South American fur seal, Arctocephalus australis, has been exploited in Peru by humans since ca. 2000 BC (Bonavia, 1982) and populations were nearly extirpated by indiscriminate commercial hunting from the early 1900s until 1946. According to Majluf (1987a,b), sealing of this species in Peru was totally banned in 1959, but poaching nevertheless continued to occur at a lesser level.

The national census conducted by IMARPE (Instituto del Mar del Perú) along the Peruvian coast (December 1999) indicated that this population declined from 24,481 in December 1996 (Arias-Schreiber and Rivas, 1998) to 8223 individuals in December 1999 (Arias-Schreiber, 2000), as a result of low food availability due to the replacement of cold and nutrient

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0006-3207/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2006.02.017
rich waters of the upwelling system with warm, poor nutrient and low productivity waters during El Niño. Due to this drastic population decline, the Peruvian population of A. australis should be considered as a demographically bottlenecked population. Indeed A. australis is now classified as in danger of extinction in the Peruvian coast (Decreto Supremo No. 013-99-AG).

The census population size (N) is usually the only information available for most threatened species. The effective population size (Ne) is envisioned as the size of an ideal population that has the same rate of increase in homozygosity or gene frequency change as the actual population under consideration (Wright, 1931). For evolutionary matters, the effective population size, not the census number, is a prime concern. Factors such as variation in the sex ratio of breeding individuals, variation of population size in different generations, and variation of mating system (e.g., polygynies versus polyandrous) may be important (Hedrick, 2000), and can be accounted for the estimate of the effective population size.

Here we present the first estimate of Ne of the Peruvian population of A. australis that takes into account the effects of (a) the mating system (and resulting skew in sex ratio variation), and (b) variation in population size caused by the most severe El Niño event of the century (1997–1998) (McPhaden, 1999). We also comment on the consequences of this value for the conservation of a bottlenecked population.

2. Methods

In order to account for the differences in the number of breeding males and females we used data from the census conducted during 1999 by IMARPE (after the 1997–1998 El Niño event, Arias-Schereiber, 2000) which covered 22 haulout areas from Islas Chinchas (13°38’S 76°24’W) to Punta Coles (17°42’S 71°23’W) and included the most important reproductive colonies of the species on the Peruvian coast (Punta Arquillo 13°54’S 76°19’W, San Fernando 15°04’S 75°21’W, Tres Hermanas 15°26’S 75°04’W, Punta Atico 16°14’S 73°41’W and Punta Coles 17°42’S 71°23’W, Fig. 1). The census population size was of 8223 individuals and the number of breeding females was 3215 individuals, while 337 breeding males were counted (territorial (breeding) males are only the males that mate on the beach, while juveniles in reproductive age, but without a territory, do not mate and are counted as “subadults males” in the census). The South American fur seal presents a polygynic breeding system that was modified from lekking to a territorial reproductive system on the Peruvian coast, following changes in population density and availability of space for male territories (Majluf, 1987a). In both systems, a small number of males are able to mate with many females, so the effective population size should be smaller than the actual population size (Crow and Kimura, 1970). The Ne equation that accounts for the effects of unequal sex-ratio is

\[
Ne = \frac{4N_{ef}N_{em}}{N_{ef} + N_{em}}
\]

where N_{ef} is the number of breeding females and N_{em} is the number of breeding males.

In order to calculate the effect of changes in population size over time we estimated effective population sizes before and after the El Niño event. To calculate the effective population size prior to the El Niño event we used data collected for 1996–1997 by IMARPE (Arias-Schreiber and Rivas, 1998), with a census size of 24,481 individuals, among which 2903 were reproductive males and 10,720 were reproductive females. This estimate of Ne for populations before and after the El Niño of 1997–1998 was then used to estimate an overall effective population size, which accounts for the variation in

Fig. 1 – Haulout areas of South American fur seal, Arctocephalus australis, in the Peruvian coast; including census size of the reproductive population (F = adult females, M = adult males and NI = no identified) conducted in 1999 of the most important breeding colonies of the species (see text).
population size in different generations. The $N_e$ for a population that varies in size over generations is given by the harmonic mean of the $N_e$ in each generation (Hedrick, 2000):

$$N_e = \frac{t}{\sum \frac{1}{N_i}}$$

where $N_i$ is the effective population size in the $i$th generation and $t$ is the number of generations considered.

### 3. Results and discussion

The $N_e$ value that accounts for the effects of unequal sex-ratio was 1220 (year 1999) and the $N_e$ prior to the El Niño event of 1997–1998 was 9138 for the year of 1996. This yielded an overall effective population size of 2153 which accounts for both the effects of the mating system and variation in population size. If we assume that this population spends a greater proportion of generations with effective population sizes similar to that of the 1996 study (prior to the El Niño of 1997–1998) the overall $N_e$ is somewhat increased; for example, if the proportion of time spent with pre- and post-El Niño populations (as described above) is 3:1, the overall $N_e$ is approximately 2600. It is important to mention that our estimates do not include the census size of populations between 1900 and 1996. There is little information for this period, but it has been suggested that populations crashed severely, reaching a low of 40 individuals in 1951 (Piazza, 1969). Thus, our estimation results in higher $N_e$ than if data on previous generations was available.

This estimate of $N_e$ does not account for two factors: the variation in reproductive success among individuals, and the possibility that peripheral males are reproductively active. In both cases it is very difficult to obtain relevant information. However, we can discuss the likely impact of these factors upon our results. If individual variance in reproductive success exists, its effect will reduce the estimate of $N_e$ to a more conservative value. The possibility that peripheral males breed with harem females has been observed for some pinnipeds species including Southern elephant seal, *Mirounga leonina* (Hoelzel et al., 1999). In the lekking system, presented by Majluf and Trillmich (1981). Therefore, prior to 1987, numbers obtained from censuses can only be taken as rough estimates. Between 1951 and 1979, the population of *A. australis* in Peru was estimated from 40 (Piazza, 1969) to 20,255 individuals (Majluf and Trillmich, 1981). However, systematic and careful censuses conducted by IMARPE for the years 1992 and 1996 estimated the population size as 27,219 and 24,481, respectively (Arias-Schreiber and Rivas, 1998). These numbers are substantially higher than the estimate of $N_e$ of 2153 based on recent censuses. It is important to mention that errors due to personnel experience during the censuses were calculated as confidence limits for the whole studied coast, including Punta Coles which has a complicated topography for census activity. To minimize the effects of the mating system and variation in population size, it is important to mention that our estimates do not include the census size of populations between 1900 and 1996. There is little information for this period, but it has been suggested that populations crashed severely, reaching a low of 40 individuals in 1951 (Piazza, 1969). Thus, our estimation results in higher $N_e$ than if data on previous generations was available.

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The calculated $N_e$ for the Peruvian population of *A. australis* seems extremely large when compared with values for the species mentioned above. However, according to Reed et al. (2003), for 102 vertebrate species, including three pinnipeds, the minimum viable population size (MVP) calculated was on average approximately 7000 breeding age adults. The MVP can be defined as the smallest size required for a population or species to have a predetermined probability of persistence for a given length time (Shafer, 1981). All MVP estimates in the study of Reed et al. (2003) are for a 99% probability of persistence for 40 generations and the models for this estimate are comprehensive and include age-structure, the effect of demographic stochasticity, environmental stochasticity, and inbreeding depression (MacCarthy et al., 2001). The authors estimated MVP using three different criteria: the mean carrying capacity required for a 99% probability of persistence for 40 generations (MVP), the minimum viable adult population size (MVP), calculated by the software Vortex (Miller and Lacy, 1999) and the effective population size (MVP*). These three measures of MVP all correlated very strongly with each other ($r > 0.93$ in all comparisons) and the choice of measure does not qualitatively change the conclusions reached in any of the analysis. The mean $N_e$ estimated for 102 vertebrate species was 1752 individuals (SD = 156) (Reed et al., 2003), which is a very close value to the 2153 individuals estimated for the Peruvian population of *A. australis*. In this sense we believe that the estimated $N_e$ for the Peruvian population represents a critical value, because it is significantly lower than the average MVP and close to the $N_e$ values estimated for vertebrates. The MVP for other
The estimated \( N_e \) of 2153 combined with the apparently current increase in frequency of El Niño events are reasons of great concern for the survival of the species on the Peruvian coast. According to Majluf (1998), the El Niño event from 1997 to 1998 caused a high juvenile and pup mortality, as well as a high mortality of reproductive females, due to the need to spend very long periods at foraging (10–20 days), suffering subsequently from physical stress and even starvation. Although the South American fur seal population on the Pacific side of its distribution, most probably is well adapted to recurrent El Niño events, the already depleted current population may not be able to survive more events similar in magnitude to the 1997–1998 El Niño. Indeed, the continued viability of A. australis on the Peruvian coast may depend primarily on non-genetic factors, such as local availability of food resources during breeding seasons and its consequent effects on pup growth and survival. Global warming models predict stronger and more frequent El Niños in the future (NCDC-NOAA, 2004). If a strong one were to hit the surviving adults in the near future, there would be few juveniles to replace them and the future generations may will be compromised and in a much greater risk than ever imagined (Majluf, 1998). Thus, this study's estimate of a \( N_e \) of 2153 specimens should be taken into account in future management plans to ensure the conservation and protection of the species on the Peruvian coast.

**Acknowledgements**

The authors would like to thank Ignacio M.B. Moreno, who kindly prepared the Fig. 1, and Dr. Jim Hamrick for encouraging population genetics studies. To Joe Hoffman, who kindly review the final manuscript. We also thank Armando Valdés-Velasquez and one anonymous referee for the comments and suggestions. This study was financially supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grants 00/00248-2, 00/01340-0). This paper is GEMARS contribution No. 17.

**References**


