

A MODEL LIFE TABLE FOR MAGELLANIC PENGUINS (*SPHENISCUS MAGELLANICUS*) AT PUNTA TOMBO, ARGENTINA

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Abstract.—Our present knowledge of breeding biology and population dynamics of *Spheniscus magellanicus* at Punta Tombo colony are summarized. Records of eight consecutive breeding seasons showed high mortality rates of eggs (47%) during the incubation period and high mortality rates of chicks (57%) throughout the rearing stage. After independence, fledglings had high mortality rate (58%) during the first pelagic migration after which the life-expectancy of the species increased, reaching a maximum at two years old, and decreasing gradually. Considering the recoveries of marked birds for a cohort along six age-classes, and estimating that adult breeders constitute ten age-classes in the colony, a horizontal life table is proposed. The maximum life-span for the species is estimated at about 25–30 yrs.

MODELO DE SUPERVIVENCIA PARA EL PINGÜINO *SPHENISCUS MAGELLANICUS* EN PUNTA TOMBO, ARGENTINA

Sinopsis.—Se presenta un resumen sobre la biología y dinámica de la población de *Spheniscus magellanicus* en la colonia de Punta Tombo, Argentina. Los registros de ocho sucesivas estaciones reproductivas mostraron altas tasas de mortalidad de huevos (47% durante el período de incubación) y pichones (57%) a través de todo el período de crianza. Después de la independencia los volantones mostraron una alta tasa de mortalidad (58%) durante su primera migración pelágica. Posteriormente, la expectativa de vida de la especie aumenta alcanzando un máximo a la edad de dos años, para luego disminuir gradualmente. Tomando en consideración la recaptura de aves marcadas de una cohorte a lo largo de seis clases de edad, y estimando que la clase adulta reproductora está constituida por diez clases de edad, se propone una tabla horizontal de vida. La longevidad máxima de la especie es estimada entre 25–30 años.

The annual reproductive cycle of Magellanic Penguins (*Spheniscus magellanicus*) is highly synchronized in the area of this study. Since early surveys by Godoy (1963) and Boswall and MacIver (1974), this species has been intensively studied by Scolaro (1978, 1983, 1984a). Records of banded birds suggest delayed sexual maturity for both sexes and high mortality for pre-breeding age classes (Scolaro 1980, 1984a). These findings suggest a longer life-span in the Magellanic Penguin than other penguin species. However, factors delimiting some age classes are poorly known. The present paper is an attempt to construct a model life-table, with an estimation of the life expectancy of this relatively high latitude penguin.

GENERAL BIOLOGY

Spheniscus magellanicus breeds on the southern Atlantic and Pacific coasts of South America. On the Atlantic side they breed from 42° south

latitude almost to Cape Horn, including the Malvinas (or Falkland) Islands. There are 21 recognized breeding colonies along some 1500 kilometers of continental coast and small offshore islands. On the Pacific coast, the species ranges from 29° southward (Araya 1983); its status and population on southern Chile and Tierra del Fuego archipelago remain poorly documented.

Males of the Magellanic Penguin arrive at the Punta Tombo colony during the last week of August. Each male re-establishes itself in its nest-site of the previous year. Females arrive between the second and third week of September. Laying begins in the last week of September and has never been observed after the third week of October. Birds that lose the first clutch are unable to lay a second, a limitation that represents one of the main differences between this species and other species of the genus *Spheniscus* (Araya 1983, Shelton et al. 1984).

A clutch normally contains two eggs of nearly equal size (74 × 55.5 mm) and weight (127 g). Incubation lasts 40 d and hatching begins during the first week of November (Scolaro 1978, 1984a). In Magellanic Penguins the male fasts 2–3 wks before laying while occupying and defending his nest. His reserves almost exhausted, he returns to the sea leaving the first incubation shift (21 d) to the female. This shift represents about 50% of the total period. The male takes the second shorter shift, and a third short shift by the female allows the male to go to sea and return with food for the chicks. Timing of nest relief appears to be extremely important; delays caused by the failure of the non-incubating partner to return are the main cause of nest desertions with loss of clutches to predation. The mean mortality rate of eggs was 47% and the mean mortality rate of chicks, from hatching to fledgling was 57%. Both rates can be related to nest-density distribution in the colony (Scolaro 1983, 1984a,c).

The interval between laying of the first and second egg varies from 11.5 h to 4 d, with a consistently staggered hatching. By the time the second chick is hatched the first is appreciably larger, heavier, and more efficient in obtaining food from its parents. When food is scarce, the second chick often goes hungry and may die of starvation. Second chicks are lost from a high proportion of nests; during the 1978–1979 breeding season at Punta Tombo, sibling chicks were successfully reared in only 17% of the nests (Scolaro 1983, 1984a).

The rearing stage is longer in Magellanic Penguins than in other temperate penguins. Scolaro (1983) recognizes two stages, the guard stage (20–23 d) and the creche stage (60–85 d). Fledglings start to leave the creches for the shore in the first week of February, after they shed their down and acquire the yearling plumage. As soon as rearing is finished, moulting and fasting of adults begin; by mid-April, all adults have completed their moult and starting their annual pelagic migration to the southern coast of Brasil and the Rio de la Plata estuary (Scolaro 1983, 1984a,b).

Recoveries of marked birds enabled me to determine the age of sexual

maturity. Females begin breeding in the fourth year (12.8%) whereas males begin in the fifth year (30.7%), although the percentage of successful breeding attempts increases one year later in both sexes (Scolaro 1984d).

On the basis of a previous survey (Scolaro et al. 1981), population dynamics at the Punta Tombo colony were modelled by simulation, based on density dependent mechanisms of variation in mortality rates for each age class. Analysis by means of this model satisfactorily agrees with the cyclical trends observed in the field.

STUDY SITE

This study was centered in Punta Tombo (44°02'S, 65°10'W), the southern boundary of Janssen Bay, in the Chubut Province of Patagonia, Argentina. This bay is limited by two points, Punta Clara to the north and Punta Tombo to the south. On both these points, the Magellanic Penguins nest in two long separate colonies.

The coast is formed by marine sediments, which were deposited in the middle Tertiary Period ("Patagoniense") over a background of pre-Jurassic crystalline rocks, principally quartz porphyry. A wide, low platform, ringed with glacial boulders and covered by silt, washed down from the inland terraces, provides easy access from the sea and a large, soil-covered area suitable for nesting sites of Magellanic Penguins. The unusual topography may explain the presence of the two greatest concentrations of these birds.

Punta Tombo lies in the Central District of the phytogeographical Patagonian Province. Dominant vegetation on the strand flats and lower terraces is *Chuquiraga avellanadae*. Near the coast, there are patches of *Schinus molle*, *Suaeda divaricata* and *Lycium ameghinoi*, forming dense shrubs or bushes and providing shade and cover for the penguin nests. The grass community on sandy dunes does not provide shelter, however, it is often used as nesting material.

The nesting area is irregular in shape, following the coastline. It occupies approximately 4–5 km of shoreline, extending inland over 303.4 ha and accommodating over 397,000 nests (approximately 794,000 breeding birds) during each reproductive season. The average overall density was 1561 nests/ha (Scolaro and Arias de Reyna 1984). The peripheral areas of low nest-density (1–5 nests/100 m⁻²) represented 23.8% of the area; those of average to low nest-density (6–25 nests/100 m⁻²) represented 63%; those of medium nest-density (26–60 nests/100 m⁻²) represented 10.8% and those of high nest-density (61–100 nests/100 m⁻²) represented only 2.2%.

The spatial distribution of nests is clumped showing a decreasing gradient from the coast to inland. Greater or lesser nest-density is closely related to the soil texture and distance from the sea (food source) in areas of medium density. In other areas, protection from aerial predators and sun become more important factors in determining the distribution of nests. Greatest densities are found in clay or sandy-clay soils close to the shore, where burrows predominate. Away from the shore, where the

sediments are thinner and rock fragments more plentiful, burrow nesting is less common and more nests are found in the open under bushes, but lower density is the rule. The bushes provide protection from intense predation by gulls and skuas nesting close by.

METHODS

A marking program began in the 1978–1979 breeding season, when 2000 chicks were banded just before fledgling. Because of the high mortality rate of fledglings, we banded only yearlings from 1979 to 1985. We marked 1000–2000 yearlings/yr. In Magellanic Penguins, yearlings keep their distinctive immature plumage and characteristic behavior, and can be readily recognized when they return to the colony at the end of their first year (Scolaro 1978, 1980).

The yearlings were herded in groups into funnel traps, usually on the beach or into caves or other natural enclosures when they could be held temporarily. They were marked with metallic and colored plastic rings, also numbered, that tightly encircled the wing at the shoulder; none caused distress or damage of any kind. In one season, successful fledglings were marked with aluminum rings encircling the tibio-tarsus at the right leg. These proved difficult to see at a distance and several birds were injured, so the practice was discontinued. Later, when a foot-marked bird was sighted, it was caught and rebanded with a plastic ring.

Bands were large enough to be read with 7×50 binoculars from a distance of 10 m. When necessary, the birds were caught by means of a curved hook that looped around their “ankles” (articulation of the tibio-tarsus and tarso-metatarsus bones).

Daily observations were made from September to the end of March during the breeding cycles of 1978, 1980, and 1982–1985, and by means of weekly visits of 3–4 d during the same periods of 1979 and 1981.

The plastic rings proved successful and band loss was rare. However, when necessary, the data of the present study were adjusted using the formula proposed by Ainley and DeMaster (1980).

In order to construct the life table, I have followed the method suggested by Rabinovich (1980) for cases of populations in which the ages of individuals cannot be distinguished (in our case, the adult breeders). To generate survivorship curves the method takes into account the duration of a stage or phase in the cycle, establishing a relationship between the number of individuals found at each stage of development. Each stage consists of a group of age classes and for that reason can be adapted to the obtained records. The technique assumes a stable population during the study. Migration from the study area cannot be documented; there are a few records of young birds wandering from Punta Tombo to neighbouring colonies but they eventually return to their natal colony to breed.

The survivorship curve was fitted by least squares. The model assumes that: 1) sexual maturity occurs (and breeding) after the fourth year in females and fifth in males; 2) ten active breeder classes are considered (ages 4–14) and these birds constitute the total number of adult birds

TABLE 1. Partial horizontal life table for the Magellanic Penguin. Data were averaged over the years of recovery (1979–1985).

Age (yr)	Number banded as chicks	Number recovered at age indicated	Recoveries as a proportion of those banded
1	1797	765 ^a	0.426
2	2200	930 ^b	0.423
3	3095	88	0.028
4	3975	87	0.022
5	2775	56	0.020
6	1895	33	0.017

^a # calculated from Scolaro (1980).

^b Calculated from Scolaro (1983).

estimated in a given year: the model uses the average of the period 1976–1980 (Scolaro et al. 1979, 1981); 3) due to the difficulty in identifying them, three-year-old birds are considered members of the adult population counted in the above mentioned census; 4) the survivorship curve, plotted from hatching to six years old, assumes similar death-rates for males and females, and 5) the death-rates proposed by the model were adjusted for adult breeders using the minimum death-rate, as calculated by the Service method (Rabinovich 1980). The method is based on the assumption that the death-rate within a given stage remains constant. Although such an assumption is questionable, we preferred to accept this condition since the annual pelagic migration of Magellanic Penguins prevents identification of partial death-rates and their causes. Moreover, we are mostly interested in the total death-rate for a given age class over one year. Estimates of the theoretical number of individuals starting life in each stage are made on the basis of the above mentioned prerequisites.

RESULTS

Table 1 shows the recovery data of various cohorts corrected for individual records; this is a partial horizontal life table constructed from data that were averaged over the years of recovery. The data were used to generate a survivorship curve (Fig. 1) for the first six age classes. The curve was fitted by least squares and is described by the equation

$$Y = 0.93e^{-0.77X}$$

where Y is the proportion surviving, X is the age of bird in years, e is the natural logarithm.

By extrapolation from this equation the maximum longevity of the species is between 24–26 yrs.

In constructing the life table model, the values considered in plotting a negative exponential curve are shown in Table 2. Census data and estimates from Scolaro et al. (1979) and Scolaro (1983) were based on the original cohorts of chicks hatched in the 1978 and 1979 breeding seasons.

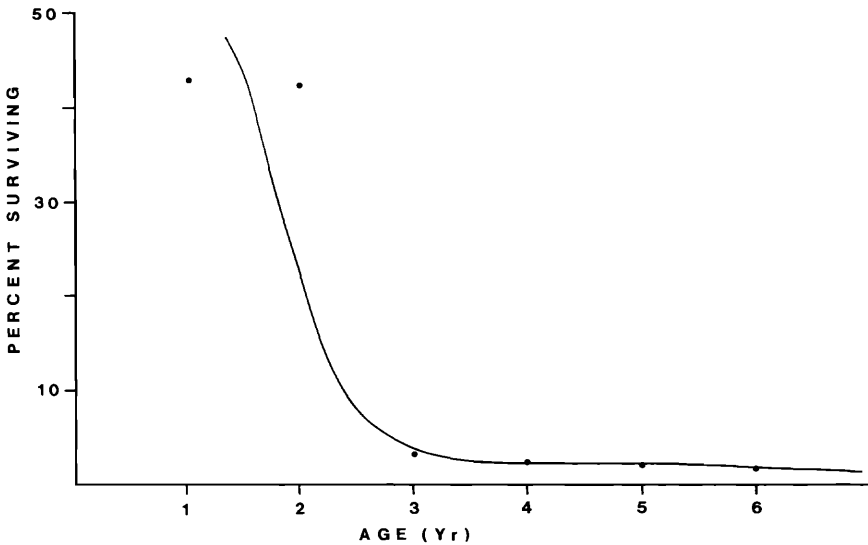


FIGURE 1. Magellanic Penguins survivorship curve at Punta Tombo. The data points, from Table 1, were used to generate the curve fitted by least squares: $y = 0.93e^{-0.77x}$.

The final model fitted by the least squares method corresponds to the equation

$$Y = 309030e^{-0.0009X}$$

Table 3 is a life table based on the above survival equation and Figure 2 shows the corresponding life-expectancy curve together with similar curves for Yellow-eyed (*Megadyptes antipodes*) and Adelic (*Pygoscelis adeliae*) penguins drawn from Ainley and DeMaster (1980). Analysis of this curve shows that in the Magellanic Penguin, life-expectancy increases considerably after the initial hazards of rearing and the first pelagic migration, reaching a maximum of 9.79 yr about the end of the second year. After surviving birth and rearing, where eggs have a mean failure of 47% and chicks a mortality rate of 57%, the fledgling will subsequently have a pelagic migration with its high mortality (57.9%; Scolaro 1980).

TABLE 2. Estimation of population structure for the Magellanic Penguin at Punta Tombo colony. Data were based on the cohorts hatched in 1978 and 1979 breeding seasons.

Stage	Number	Stage duration (d)	Adjusted density
I Eggs	633,255	40	15,831.4
II Fledglings	186,209	180	1034.5
III Yearlings	81,932	365	224.5
IV Breeders	764,471	4015	190.4

TABLE 3. Vertical Life Table for the Punta Tombo colony based on the survival curve:
 $Y = 309,030e^{-0.0099X}$.

Age (yr)	Number of penguins	Proportion surviving	Deaths within age-class	Mortality within age-class	Mean survivorship to next age-class	Time-life remaining of survival	Life expectancy (yr)
0	633,255	—	447,046	0.71	0.647	2.359	2.36
0.5	186,209	0.294	68,209	0.37	0.240	1.712	5.82
1	118,000	0.186	33,000	0.28	0.160	1.472	7.91
2	85,000	0.134	5000	0.06	0.130	1.312	9.79
3	80,000	0.126	4000	0.05	0.123	1.182	9.38
4	76,000	0.120	3000	0.04	0.118	1.059	8.83
5	73,000	0.115	3000	0.04	0.113	0.941	8.18
6	70,000	0.110	5000	0.07	0.107	0.828	7.53
7	65,000	0.103	2000	0.03	0.101	0.721	7.00
8	63,000	0.099	3000	0.05	0.097	0.620	6.26
9	60,000	0.095	5000	0.08	0.091	0.523	5.50
10	55,000	0.087	5000	0.09	0.084	0.432	4.96
11	51,000	0.081	4000	0.08	0.079	0.348	4.30
12	48,000	0.076	3000	0.06	0.074	0.269	3.54
13	45,000	0.071	3000	0.07	0.069	0.195	2.75
14	42,000	0.066	3000	0.07	0.064	0.126	1.91
15	39,000	0.062	3000	0.08	0.062	0.062	1.00

At or after 4 yrs old sexual maturity is attained and breeding begins; thereafter life expectancy falls steadily with advancing age.

The death/survival ratio, a measure introduced by Bess (1945) shows how the population would have increased in the absence of a given mortality factor. It is, in other words, an indirect measure of the minimum death-rate. We have calculated this index (0.95) for adult breeder classes (4th to 14th) as the rate between the mortality operated from 4th to the end of 14th age class and the survivorship of 14-year-olds (the end of adult breeder category) (see Table 3, where $76,000 - 39,000/39,000 = 0.95$). In consequence, the minimum mortality for each breeding age class was estimated at 0.08 (0.95/11), assuming a stable population.

DISCUSSION

Both equations predict a similar lifespan for Magellanic Penguins, calculated as a maximum between 25–30 yrs. Such an age seems reasonable for a species in a temperate to cold climate (Stonehouse 1970) and is consistent with values recorded in zoos and with the calculated longevity of the Yellow-eyed Penguin (Ainley and DeMaster 1980).

The yearling and immature periods, with their high mortalities, are the periods of most intense selection and probably limit population growth. This corroborates a previous demographic survey of the Punta Tombo colony (Scolaro et al. 1981). An above normal mortality among immature birds over three consecutive breeding cycles would severely distort the

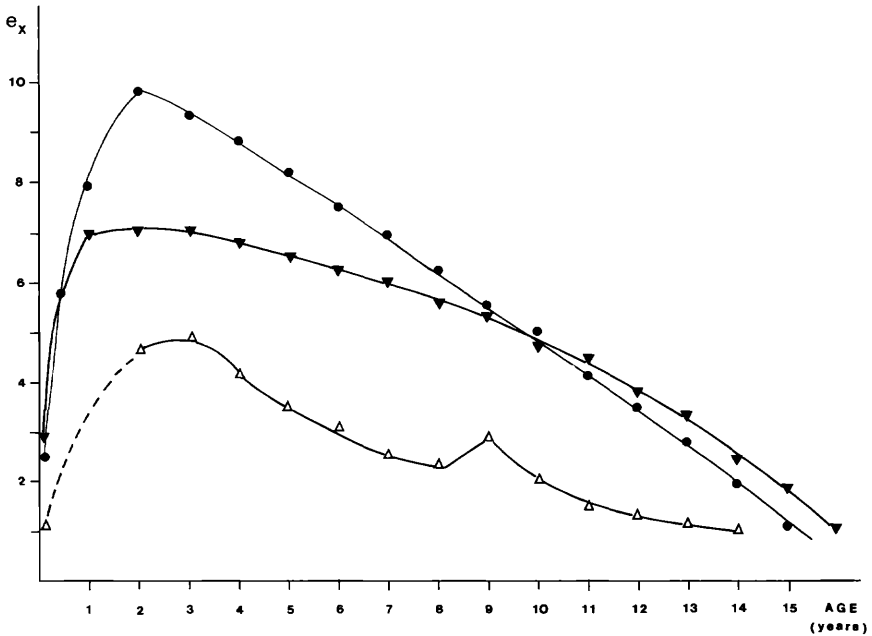


FIGURE 2. Life-expectancy curves. Closed circles are Magellanic Penguin; Closed triangles are Yellow-eyed Penguin; Open triangles are Adelic Penguin (dotted line indicates extrapolation of data; from Ainley and DeMaster 1980). Life-expectancy (e_x) in years.

demographic curve. High death-rates among immatures have frequently been reported for various penguin species (Davis 1982, Shelton et al. 1984).

Common to all three species, represented in Figure 2, is a marked increase in life-expectancy at maturity, which occurs earliest in the Yellow-eyed Penguin (at one year), about one year later in the Magellanic Penguin, and two years later in the Adelic Penguin. The gentler slope of the curve in Yellow-eyed Penguins illustrates the lower death-rates established for that species. The Adelic curve indicates the shortest life and highest mortality rates. The slight peak at 9 yrs old, if real, suggests a surmounting of a mortality risk at this age, and subsequent increase in life expectancy. The change may result from higher mortality among females and the preponderance of males among older cohorts (Ainley and DeMaster 1980). The curve for the Magellanic Penguin more closely resembles that of the Yellow-eyed Penguin, another temperate species, both of which are characterized by high mortality rates after the age of fifteen.

In calculating the life table I used the minimum death-rate for adult breeder classes. According to Rabinovich (1980), some authors question the assumption of a constant death-rate regardless of changes in population density. Nevertheless, if, as is supposed, the deaths occurring after

a given stage are in some way related to that stage, the index enables us to assess the relative effect of various death-rate factors in a given stage. Once the factors operating simultaneously are known, the minimum mortality can be corrected, and a more real expression can be obtained for each age class.

Recently, Shelton et al. (1984) used a life table for the Jackass Penguin (*Spheniscus demersus*) in order to compute the first-year survival necessary to achieve the observed growth in some penguin colonies in South Africa. The biology and behavior of this species are not comparable to Magellanic Penguins. However, some assumptions successfully supported in this model, such as mortality of chicks and identification of critical age-classes (2- and 3-year-olds) affecting population growth, were similar to the model proposed for Magellanic Penguins.

The present study has been unable to separate some of the density dependent factors affecting mortality, but the analysis enables us to identify the mortality of each age. Considering that Magellanic Penguins do not breed until the fifth year (average of males and females), and the records of consecutive successful matings (7 seasons) and alternate-mating-resting years (8-9 yrs; two records), the model is consistent with an expectation of many years of breeding and extended longevity for the species (at least 25 yr).

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