

ACTAS DE LA ACADEMIA NACIONAL DE CIENCIAS. (CORDOBA, ARGENTINA)
TOMO XIV, DICIEMBRE DE 2008

TWO-SEX POPULATION MODELS APPLIED TO POLYGYNOUS SPECIES

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TWO-SEX POPULATION MODELS

Keywords: population dynamics, social structure, sex ratio, elephant seal.

MODELOS POBLACIONALES DE DOS SEXOS

Palabras clave: dinámica poblacional, estructura social, proporción sexual, elefante marino del sur.

MODELOS POBLACIONALES DE DOS SEXOS APLICADOS A ESPECIES POLIGÍNICAS

SYNOPSIS

We review a two-sex population model and focus on the link between demography and social structure in a polygynous species. The model was applied to the southern elephant seal population of Península Valdés, one that shows contrasting trends in two demographic subunits with distinct social structure. This approach provides a general framework to include social variables into population dynamics. This perspective extends the scope of standard linear models and adds a tool that identifies the relative effect of changes in number of one sex on the population.

SINOPSIS

En este trabajo revisamos un modelo poblacional de dos sexos enfocándolo en la relación entre demografía y estructura social para una especie poligámica. El modelo fue aplicado a la población de elefantes marinos del sur de Península Valdés, una población que muestra tendencias contrastantes en dos subunidades con distinta estructura social. Este enfoque provee un marco general que permite incluir variables sociales en la dinámica de poblaciones como una extensión del modelo lineal estándar y aporta una herramienta al análisis de la dinámica identificando las influencias relativas de cada sexo.

INTRODUCTION

Animals in general and mammals in particular, neither disperse nor relate to one another randomly, but form dynamic relationships of varying number, complexity and duration. These patterns of association and interdependence are referred to as social structure, and affect survival and reproductive strategies. In gregarious and polygynous animals, individual hierarchies and the structure of a group influence life-history parameters. The effects of social structure on population parameters will then have demographic consequences (Young and Isbell 1994, Milner-Gulland *et al.* 2003). Consequently, including aspects of the social structure in demographic models may help to better interpret population dynamics and then used them in conservation applications (Gerber 2006). It could also facilitate the identification of links between changes in social parameters (e.g., group size, sex ratio, and mating behavior) and population parameters (e.g., status, trends, dynamic behavior).

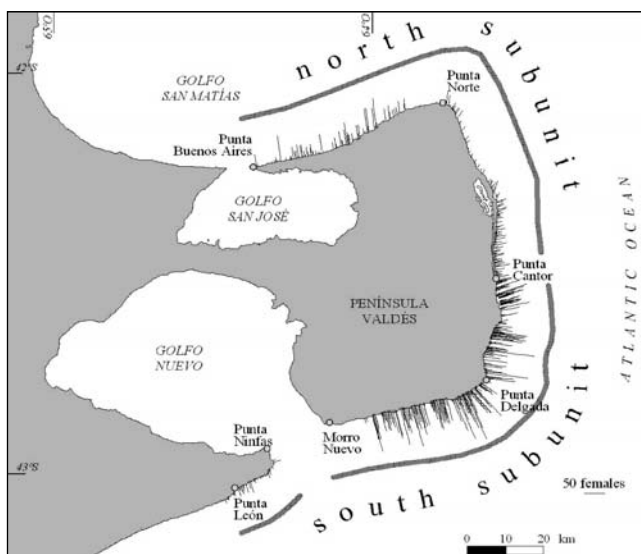


Figure 1. Distribution of seals at PV and nearby areas. (subunit North and South indicated by the thick grey line following the contour of the coast) Thin lines provide an idea of harem sizes, length line is proportional to the number of females in the harem according to a scale given in the map. Harem location was georeferenced during the 2006 survey.

We analyze and apply a two-sex model to understand the relationship between some social parameters and the dynamics of a polygynous population. We seek to advance in conservation with a model of predictive value that may help understand how practical observations (harem size) could be important in population model. To anchor our explorations to the realities of natural systems, we analyze data for the southern elephant seal, *Mirounga leonina*, population of Península Valdés, Argentina.

Why this species?

Southern elephant seals are marine mammals that have an annual cycle with two well-defined pelagic phases, intercalated between molt and reproduction (Le Boeuf and Laws 1994). Adult males and females reproduce ashore in September - October, and provide one of the most extreme examples of polygyny in a mammal (Le Boeuf and Laws 1994, Campagna *et al.* 1993). The social units are harems integrated by a single dominant male that monopolizes access to sexually receptive females; these harems may vary in size from few up more than 100 females at peak breeding season.

Adult male elephant seals can be up to five times larger than reproductive females. In addition, differences between sexes are evident in the parameters of the breeding and foraging behavior, and life history strategies (Hindell *et al.* 1991, Campagna *et al.* 1998, 1999). Breeding females haul-out for about 30 days, during which they fast and give birth to one pup per year. After about 20 days of lactation, females mate and get pregnant. Adults and subadult males haul-out and fast during 6-8 weeks. Dominant males attempt to inseminate as many females as possible and keep all other males away, whereas lower rank males take up peripheral positions in the harems and mate opportunistically (Le Boeuf and Laws 1994).

Why this population?

The seal population of Peninsula Valdés (PV) has been studied from a demographic and social behavior perspective for the last 25 years (Campagna and Lewis 1992, Baldi *et al.* 1996, Lewis *et al.* 1998). Annual surveys of this population have been conducted since 1995 during the peak of the breeding season (first week of October) when about 96% of all breeding females found ashore. Surveys encompass the whole breeding area, which extends for 200 km of coast on the Atlantic front of PV, between Punta Buenos Aires and Morro Nuevo, and for 60 km south of the peninsula, between Punta Ninfas and Punta León (Figure 1). Two demographic subunits have been identified in the North (between Punta Buenos Aires and Punta Cantor) and South (between Punta Cantor, Morro Nuevo, Punta Ninfas and Punta León) of PV, respectively, with different trends (increasing at South and decreasing at North), mean harem size and sex ratio (Figure 2). PV population is unique in terms of the expanding range of utilization of the coast and increase in the number of births. However, within the colony, the northern and southern sides are like different populations. In the following sections, we described a two-sex model, for a general polygynous population, that was developed taking into consideration the biological characteristics of elephant seals and the kind of data available for the PV population.

BASIC HYPOTHESES AND MODEL STRUCTURE

We consider a stage-based, density-independent model (Figure 3), similar in its general formulation to those described in Caswell (2001), and place it in the context of social structure. Five age categories are defined for the model: **newborn pups**, **subadult females**, **adult females**, **subadult males** and **adult**

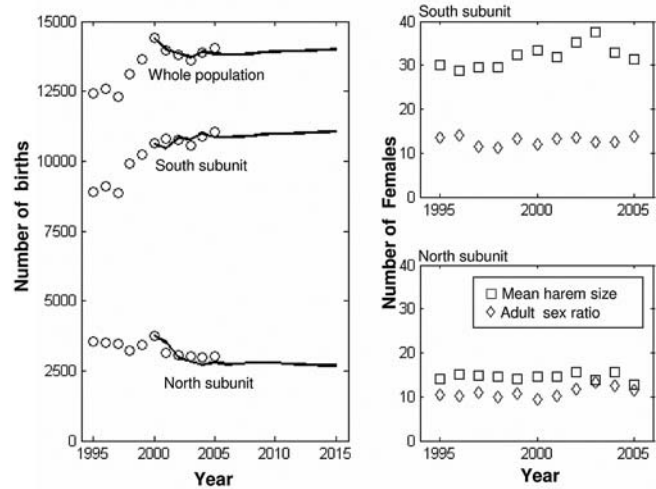


Figure 2. Left box: number of births observed for the whole PV population and the two demographic subunits. Lines correspond to model projections. Right boxes: social structure for the two subunits represented by annual mean harem size and adult sex ratio (mean number of adult females per adult male).

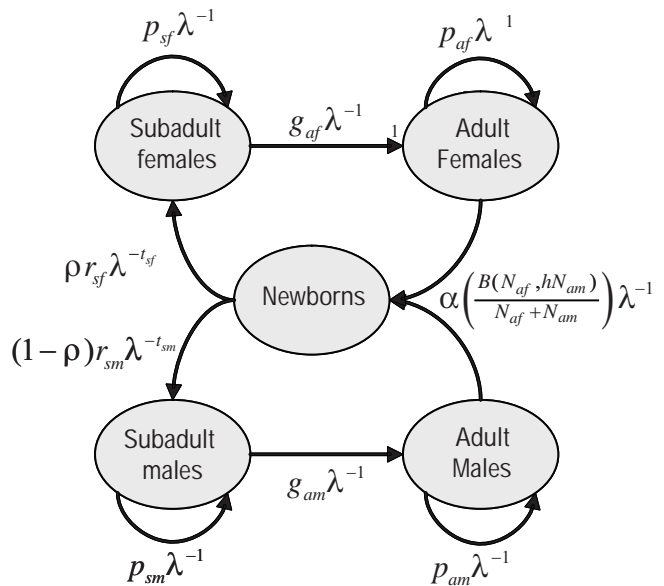


Figure 3. Life cycle z-transformed graph for the two-sex model (Caswell 2001). Exponents on λ indicate the time interval required for the transition.

males. The transition interval is one year. Females require t_{sf} years and males t_{sm} years to grow from newborn pups to subadult age categories. The transition parameters are recruitment to the subadult stages (r_{sf} , r_{sm}), the probability of surviving and remaining in the subadult stage (p_{sf} , p_{sm}), the probability of surviving and growing into the adult stage (g_{af} , g_{am}) and adult survival probabilities (p_{af} , p_{am}).

The mating system is modeled by means of the function $B(N_{af}, h.N_{am})$ which determines the number of expected matings, and represents a compromise between the number of adult females, N_{af} , and the male mating potential, $h.N_{am}$, where h is the harem size (average maximum number of females that a male can successfully mate) and N_{am} is the number of adult males. This function times the constant a , a female fertility parameter that we will call natality, yields the number of births in one breeding season as a function of the number of adults of both sexes in the previous season. The primary sex ratio (relative proportion of females at birth) is given by the constant ρ . We assume that B is a homogeneous function of degree one (Pollard 1997, Caswell 2001), thus the model is frequency dependent. Moreover, for a vast range of functions B , the population converges to an equilibrium structure, independently of the initial conditions, and grows exponentially with growth rate $\lambda = \exp(r)$, where r is the intrinsic rate of increase in Lotka's equation (Nussbaum 1989).

The model life cycle can be represented by the following system of finite difference equations where $N_p(t)$, $N_{sf}(t)$, $N_{af}(t)$, $N_{sm}(t)$ and $N_{am}(t)$ represents the number of newborn pups, subadult females, adult females, subadult males and adult males respectively, at time t :

$$\begin{aligned} N_p(t) &= \alpha B(N_{af}(t-1), hN_{am}(t-1)) \\ N_{sf}(t) &= \rho r_{sf} N_p(t-t_{sf}) + p_{sf} N_{sf}(t-1) \\ N_{af}(t) &= g_{af} N_{sf}(t-1) + p_{af} N_{af}(t-1) \\ N_{sm}(t) &= (1-\rho) r_{sm} N_p(t-t_{sm}) + p_{sm} N_{sm}(t-1) \\ N_{am}(t) &= g_{am} N_{sm}(t-1) + p_{am} N_{am}(t-1) \end{aligned} \quad (1)$$

MATING SYSTEM AND CRITICAL HAREM SIZE

We assessed the influence of the harem size on the growth rate and the equilibrium structure of the population, particularly on the adult sex ratio. The

growth rate and the equilibrium structure can be obtained from the system (1). In particular, we can see that:

$$\lambda = \alpha B(N_{af}(e), hN_{am}(e)), \quad (2)$$

where $N_{af}(e)$ and $N_{am}(e)$ give the number of adult females and adult males per newborn at equilibrium, and the sex ratio is given by:

$$\frac{N_{af}(e)}{N_{am}(e)} = \frac{\rho r_{sf} g_{af}}{(1-\rho) r_{sm} g_{am}} \frac{\lambda^{t_{sm}-t_{sf}} (\lambda - p_{sm})(\lambda - p_{am})}{(\lambda - p_{sf})(\lambda - p_{af})}. \quad (3)$$

These equations must be solved simultaneously to obtain λ and the equilibrium sex ratio (Caswell 2001). If the mating function is $B = N_{af}$ we have a female-dominant linear model; the constant a is then called adult female fertility and represents the number of births in one breeding season per adult female in the previous season. Similarly, if $B = h.N_{am}$, the model is male-dominant. In order to set the mating function, a standard option is to consider that the number of matings is determined by the less abundant sex (Bessa-Gomes *et al.* 2004); this is the minimum (Min) model:

$$B_{\text{Min}} = \text{Min}(N_{af}, h.N_{am}).$$

We also consider the maximum model:

$$B_{\text{Max}} = \text{Max}(N_{af}, h.N_{am}),$$

this coincides with model dominated by the more abundant sex.

The following remarks summarize important properties of first-degree homogeneous mating functions in relation to one sex models and harem size, and generalize similar results of Legendre *et al.* (1999). Let λ_F , λ_M denote the growth rate of the female and male dominant model, and let hc the sex

ratio at equilibrium for the female dominant model, called *critical harem size*.

Remark 1. At equilibrium, the minimum model coincides with the one sex model that has the smallest growth rate and maximum model coincides with the one sex model that has the largest growth rate.

Remark 2. Three cases can be recognized:

- I) $h > hc$, then $\lambda_F < \lambda_M$ and Min model is female dominant at equilibrium state. It regards to an equilibrium state with enough males to mate all females.
- II) $h < hc$, then $\lambda_M < \lambda_F$ and Min model is male dominant at equilibrium state. It matches with a shortage of males.
- III) $h = hc$, then $\lambda_F = \lambda_M$ and Min model coincides with Max model at equilibrium state.

Remark 3. Suppose $B(x,y)$ is a homogeneous of degree one non-decreasing function of x and y , and suppose that $B(1,1) = 1$. Then

$$B_{\text{Min}}(N_{af}, hN_{am}) \leq B(N_{af}, hN_{am}) \leq B_{\text{Max}}(N_{af}, hN_{am}).$$

If the model converges to an equilibrium state with growth rate λ , then $\lambda_{\text{Min}} \leq \lambda \leq \lambda_{\text{Max}}$.

Proofs of the Remarks

We first proof **Remark 1**. That $\lambda_{\text{Min}} \leq \lambda_{\text{Max}}$ is a direct consequence of (2). Let $\lambda_{\text{Min}} = \alpha \text{Min}(N_{af}(e_{\text{Min}}), hN_{am}(e_{\text{Min}}))$ and suppose $N_{af}(e_{\text{Min}}) \leq hN_{am}(e_{\text{Min}})$, then $\lambda_{\text{Min}} = \alpha N_{af}(e_{\text{Min}})$. However, this corresponds to growth rate of a female dominant model, thus $\lambda_{\text{Min}} = \lambda_F$. Consider now $\lambda_{\text{Max}} = \alpha \text{Max}(N_{af}(e_{\text{Max}}), hN_{am}(e_{\text{Max}}))$, if $N_{af}(e_{\text{Max}}) > hN_{am}(e_{\text{Max}})$ then $\lambda_{\text{Max}} = \lambda_F$ and $N_{af}(e_{\text{Max}}) = N_{af}(e_{\text{Min}})$, $N_{am}(e_{\text{Max}}) = N_{am}(e_{\text{Min}})$ which contradicts the assumption above. Thus $N_{af}(e_{\text{Max}}) \leq hN_{am}$

(e_{Max}) and $\lambda_{\text{Max}} = \lambda_M$, it is to say that minimum model coincides with a female dominant model at equilibrium and maximum model coincides with a male dominant ones. On the other hand, if $hN_{am}(e_{\text{Min}}) \leq N_{af}(e_{\text{Min}})$ one can see analogously that minimum model is male dominant and maximum model is female dominant at equilibrium.

To prove **Remark 2** recall that $hc = \frac{N_{af}(e_F)}{N_{am}(e_F)}$ correspond to equation (3) with $\lambda = \lambda_F$. Then $\lambda_F = \alpha N_{af}(e_F) = \alpha hc N_{am}(e_F)$, which implies that λ_F is the growth rate of a male dominant model with mean harem hc . Now, it is clear from (2) that the growth rate of a male dominant model is a non-decreasing function of h , and thus we have the three stated cases. **Remark 3** follows from B properties since that

$$\begin{aligned} B(N_{af}, hN_{am}) &= \\ &= \text{Max}(N_{af}, hN_{am}) B\left(\frac{N_{af}}{\text{Max}(N_{af}, hN_{am})}, \frac{hN_{am}}{\text{Max}(N_{af}, hN_{am})}\right) \\ &\leq \text{Max}(N_{af}, hN_{am}) B(1,1) = B_{\text{Max}}(N_{af}, hN_{am}) \end{aligned}$$

and then, if the model converges to an equilibrium state, equation (2) implies $\lambda \leq \lambda_{\text{Max}}$. The left inequality follows in the same way. At last, we note that these Remarks, as well as equation (2), do not depends of the particular form of the life cycle and remain valid in any two sex model with a single reproductive stage for each sex.

A PARAMETERIZATION OF THE MATING FUNCTION

In this section, we intend to go beyond the simple male and female dominant models to represent fertility as a smooth function of adult sex ratio. Given a harem size h , the number of mating events will be primarily limited by a shortage of females (or excess of males) whenever $N_{af} < hN_{am}$ and will be limited by a shortage of males (or excess of females) whenever $N_{af} > hN_{am}$. The extent to which matings are limited as a function of N_{af} and hN_{am} will depend

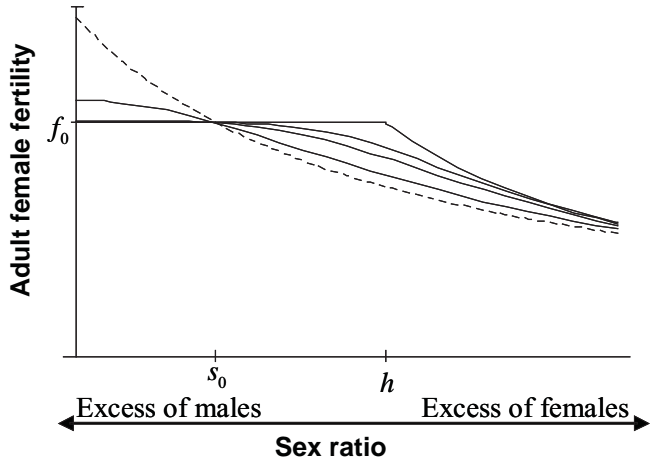


Figure 4. Adult female fertility $\propto B_M(N_{af}, hN_{am})/N_{af}$ as a function of sex ratio. We have fixed a mean sex ratio s_0 with excess of males and a mean fertility f_0 . Then the parameter a measure the influence of sex ratio on the number of births form $a = -\infty$ (minimum, no influence unless sex ratio greater than h) to $a = -1$ (harmonic mean, dashed line). Intermediate values correspond to $a = -6, -4$ and -2 .

on the shape of the function B . A way to model the influence of each sex in this process is by considering a family of generalized mean functions:

$$B_M(N_{af}, hN_{am}) = \left(\frac{1}{2}(N_{af})^a + \frac{1}{2}(hN_{am})^a \right)^{1/a},$$

where a is a real number. Extreme cases $a \approx -\infty$ and $a \approx +\infty$ correspond to the minimum and maximum functions seen before and values of a between $-\infty$ and -1 correspond to intermediate cases in between the minimum function and the harmonic mean. Actually $\propto B_M(N_{af}, hN_{am})/N_{af}$ is the adult female fertility, which is a function of the relative number of males and females (Figure 4). We propose the family of mating functions B_M as a tool to quantify the effects of the sex ratio on birth numbers. These functions are general enough when its parameters are made to vary, so as to embrace a wide range of possible situations between weak (a tending to $\pm\infty$) and strong (a close to 0) influence of the sex ratio on population trend.

APPLICATION TO PV SOUTHERN ELEPHANT SEAL POPULATION

From annual populations surveys, we collect counts of weanlings, adult females, adult males and subadult males. Then, the total number of births was calculated as the number of adult females plus the weanlings (Boyd *et al.* 1996), and the annual mean harem size was calculated as the average number of females per harem.

Parameter estimation

The proportion of females and males at birth was $\rho = 0.5$ (Campagna and Lewis 1992). Recapture of tagged animals showed that female sexual maturity occurs at age 4 (Lewis and Campagna unpublished data). Young, pre-reproductive females do not haul-out during the breeding season, so for the application of this model we considered the direct transition from newborns to adult females ($t_{sf} = 3$, $p_{sf} = 0$). Males reach the subadult stage at the age $t_{sm} = 6$ and stay in that category for 4 years more (Lewis and Campagna, unpublished data). Recruitment from newborn to adult female ($r_{sf} \cdot g_{af} = r_{af} = 0.395$) and recruitment from newborn to subadult male ($r_{sm} = 0.241$), as well as annual survival for subadult males ($s_{sm} = 0.737$) were calculated based on data from South Georgia, a stable population for which complete sex-specific life tables have been estimated (McCann 1985). Parameters p_{sm} and g_{am} were then calculated according to the formula for fixed duration stages, constant survival and equilibrium conditions (Crouse *et al.* 1987):

$$g_{am} = \frac{(s_{sm}/\lambda)^3}{1 + (s_{sm}/\lambda) + (s_{sm}/\lambda)^2 + (s_{sm}/\lambda)^3}$$

$$p_{sm} = s_{sm} - g_{am}$$

Here λ represents the population growth rate. Adult survival and natality were estimated by fitting

model predictions to observed time series of population abundance by maximum likelihood with process error (Hilborn and Mangel 1997). An unknown proportion of subadult males were not registered in surveys because these males remain at sea and do not participate in breeding. Then, we considered an expansion parameter c representing the ratio between subadult males in the population and subadult males ashore.

For the mating function, we considered the B_M family, setting parameter h to the whole population mean harem size observed over the eleven years of surveys ($h = 26$), and estimating the parameter a . The projections of the model, obtained for each year between 2001 and 2005 based on the previous 6 years, were contrasted with the corresponding numbers in surveys: $O_p(t)$, $O_{af}(t)$, $O_{sm}(t)$, $O_{am}(t)$, with a negative log-likelihood function:

$$S = \frac{1}{2\sigma_1^2} \sum_{2001}^{2005} (\ln O_p(t) - \ln N_p(t))^2 + \frac{1}{2\sigma_2^2} \sum_{2001}^{2005} \left(\frac{O_{af}(t)}{O_p(t)} - \frac{N_{af}(t)}{N_p(t)} \right)^2 + \frac{1}{2\sigma_3^2} \sum_{2001}^{2005} (\ln(c \cdot O_{sm}(t)) - \ln N_{sm}(t))^2 + \frac{1}{2\sigma_4^2} \sum_{2001}^{2005} (\ln O_{am}(t) - \ln N_{am}(t))^2 \quad (4)$$

The maximum likelihood estimates are those parameter values that minimize (4). The σ 's in equation (4) weigh the influence of different information sources and were estimated by means of an *iteratively reweighted least squares* (IRLS) method (Green 1984). We also estimated the growth rate λ iteratively and calculated the corresponding p_{sm} and g_{am} parameters. For this, we assumed initially a stationary population ($\lambda = 1$) and obtained the corresponding maximum likelihood estimates in each step recalculating then λ , p_{sm} and g_{am} according to the corresponding formulas.

Table 1. Maximum likelihood estimates and confidence intervals from likelihood profiles for the applied model.

Parameter	Confidence interval (95%)		
α	- 4.030	$-\infty$	-1.812
a	0.943	0.857	1.117
p_{af}	0.783	0.752	0.807
p_{am}	0.556	0.383	0.673
c	4.646	3.352	6.624
λ	1.001		
p_{sm}	0.627		
g_{am}	0.110		
σ_1^2	0.00009		
σ_2^2	0.00072		
σ_3^2	0.02939		
σ_4^2	0.00102		

Results

The model fit suggest a non-linear dynamics, since the point estimate of a was a finite number (Table 1). However, the minimum model ($a = -\infty$), that in this case coincides with a female dominant linear model, could not be rejected if we regarded the confidence interval of a (Table 1). The estimated growth rate was $\lambda = 1.001$, the adult sex ratio at equilibrium 11.176, and the critical harem size $hc = 10.936$. When we varied parameters α , p_{af} , and p_{am} between his confidence limits, the growth rate range from 0.973 to 1.034 and the critical harem size from 6.2 to 18.1.

CONCLUSIONS AND DISCUSSION

We develop a model assuming the male role in a polygynous species influences population growth, and integrating social structure variables as a tool to understand how individuals respond to perturbation over short time scales. The general model describes a connection between population trend and social

parameters that take into account the sex ratio (adult females per adult male) and harem size (as a measure of the operational sex ratio, Gerber 2006). We showed that, independently of the mating function shape, the sex ratio in a female-dominant model (hc), and its relation with harem size (h), is what determines the general population dynamics at equilibrium, with an excess of males if $h > hc$ and a shortage of males if $h < hc$.

In our application to elephant seals, we fitted the model to explain the observed trend, of the whole PV population, for the last 11 years (Figure 2). Results about influence of social structure are not conclusive but the B_M family of mating functions was sensitive to small differences in the sex ratio and the consequences of these differences on the number of births. Moreover, the model captured the general trend of North and South areas, when we replaced the parameter h of the mating function for the subunit mean harem size ($h = 32$ at South and $h = 15$ at North, Figure 2). The estimated critical harem size was between 6 and 18 females per adult male, that represents the baseline of reproductive potential of the population. For harem size below this value would have a lack of sufficient males to ensure that all cows are inseminated. From 1995 to 2005, the sex ratio of the PV breeding population ranged from 10.8 to 13.2 females per male and mean harem size from 22.8 to 27.9 females per male. Thus, there were enough males in the entire population to inseminate all breeding females. However, when we regard the two subunits, we find that mean harem size at

North was very close to the sex ratio and close to critical harem size too (Figure 2), in fact mean harem size at North was in the estimated range of hc , whereas mean harem size at South was out of the estimated range. Thus, differences in harem size and lack of males in the North could be related to the different trends between the subunits.

Ultimately, the application of a model that links demography to social structure in a population that easily accessed to estimate trend in numbers, provides a tool to integrate data of conservation value in a polygynous species. The most important southern elephant seal populations in the world have been either stable or decreasing sharply in the last 50 years (Hindell and Burton 1987, Pistorius *et al.* 2004). Today, some of them are apparently returning to a positive trend (Boyd *et al.* 1996, Guinet *et al.* 1999). The reasons of the difference in the trend of the populations remain unknown, but our model could be a tool to evaluate the effect on the population when a risk factor alters the sexual proportion.

ACKNOWLEDGMENTS

We specially thank to Miguel Pascual for his valuable collaboration during this work. In addition, we thank M.R. Marin for assistance in data processing and T. Fernandez for providing critical references. This work was funded by grants from the Agencia Nacional de Promoción Científica y Tecnológica (grants PICT 01-11749 and 07-06420) and Wildlife Conservation Society.

BIBLIOGRAPHY

- BALDI, R.; CAMPAGNA, C.; PEDRAZA, S. & LE BOEUF, B.J. 1996. Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. *Animal Behaviour* 51: 717-724.
- BESSA-GOMEZ, C.; LEGENDRE, S. & COLBERT, J. 2004. Alle effects, Mating systems and the extinction risk in populations with two sexes. *Ecology Letters* 7: 802-812.
- BOYD, I.L.; WALKER, T.R. & PONCET, J. 1996. Status of southern elephant seals at South Georgia. *Antarctic Science* 8: 237-244.
- CAMPAGNA, C. & LEWIS, M.N. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science* 8: 387-396.
- ; ----- & BALDI, R. 1993. Breeding biology of southern elephant seals in Patagonia. *Marine Mammal Science* 9(1): 34-47.
- ; QUINTANA, F.; LE BOEUF, B.J.; BLACKWELL, S. & CROCKER, D.E. 1998. Diving behaviour and foraging ecology of female southern elephant seals from Patagonia. *Aquatic Mammals* 4: 1-11.
- ; FEDAK, M.A. & MCCONNELL, B.J. 1999. Post-breeding distribution and diving behaviour of adult male southern elephant seals from Patagonia. *Journal of Mammalogy* 4: 1341-1352.
- CASWELL, H. 2001. Matrix population models, 2nd edn. *Sinauer Associates, Inc., Sunderland, MA, USA*.
- CROUSE, D.T.; CROWDER, L.B. & CASWELL, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68: 1412-1423.
- GERBER, L.R. 2006. Including behavioral data in demographic models improves estimates of population viability. *Frontiers in Ecology and the Environment* 4(8):419-427.
- GREEN, P. 1984. Iteratively reweighted least squares for maximum likelihood estimation and some robust and resistant alternatives. *Journal of the Royal Statistical Society B* 46: 149-162.
- GUINET, C.; JOUVENTIN, P. & WEIMERSKIRCH, H. 1999. Recent population change of the southern elephant seal at Iles Crozet and Iles Kerguelen: the end of the decrease? *Antarctic Science* 11: 193-197.
- HILBORN, R. & MANGEL, M. 1997. The Ecological Detective: confronting models with data. *Princeton University Press, New Jersey*.
- HINDELL, M.A. & BURTON, H.R. 1987. Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *Journal of Zoology* 213: 365-380.
- ; BURTON, H. & SLIP, D. 1991. Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Australian Journal of Marine and Freshwater Research* 42: 115-128.
- LE BOEUF, B.J. & LAWS, R.M. 1994. Elephant seals: An introduction to the genus, *In: Le Boeuf, B.J., and R.M. Laws (Eds.), Elephant Seals: population ecology, behavior and physiology, Berkeley: University of California Press*, pp. 1-26.
- LEGENDRE, S.; COLBERT, J.; MØLLER, A.P. & SORCI, G. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *American Naturalist* 153: 449-463.
- LEWIS, M.N.; CAMPAGNA, C.; QUINTANA, F. & FALABELLA, V. 1998. Estado actual y distribución de la población del elefante marino del sur en la Península Valdés, Argentina. *Mastozoología Neotropical* 5: 29-40.
- MCCANN, T.S. 1985. Size, status and demography of Southern elephant seal (*Mirounga leonina*) populations, *In: Ling, J.K., and M.M. Bryden (Eds.), Studies of sea mammals in South Latitudes. Northfield: South Australian Museum*, pp. 1-17.
- MILNER-GULLAND, E.J.; BUKREEVA, O.M.; COULSON, T.; LUSHCHEKINA, A.A.; KHOLODOVA, M.V.; BEKENOV, A.B. & GRACHEV, I.A. 2003. Reproductive collapse in saiga antelope harems. *Nature* 422: 135.
- NUSSBAUM, R.D. 1989. *Iterated nonlinear maps and Hilbert's projective metric, II*.
- PISTORIUS, P.A.; BESTER, M.N.; LEWIS, M.N.; TAYLOR, F.E. & CAMPAGNA, C. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology* 263:107-119.
- POLLARD, J.H. 1997. Modelling the interaction between the sexes. *Mathematical and Computer Modelling* 26(6): 11-24.
- YOUNG, T.P. & ISBELL, L.A. 1994. Minimum group size and other conservation lessons exemplified by a declining primate population. *Biological Conservation* 68: 129-134.