

Interdependence of social structure and demography in the southern elephant seal colony of Península Valdés, Argentina

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ABSTRACT

Southern elephant seals breed at Península Valdés (PV, Argentina) along 200 km of coastline. Annual pup counts at peak breeding season for the entire colony increased from 12,113 in 1995 to 14,350 in 2006. Two demographic subunits were identified in the North and South of PV with different trends in births numbers, sex ratios and harem sizes. Birth numbers increased in the South, but decreased sharply in the North. To explain the trends in the colony and subunits, a population model was proposed that integrates social structure (harem size and sex ratio) in a fertility function that quantifies the effects of the social structure on the number of births. We found that a better fit to census data results from our model compared to a linear one ($\chi^2_1 = 4.027$, $P = 0.045$). The model was then used to test alternative hypotheses about the role of recruitment and migration on the dynamic of the two subunits. Results indicated the relevance of considering social structure in population models of gregarious and polygynous species, and is an additional tool for comparative studies between populations of elephant seals where long term census are available.

Key words: Population model, fertility function, sex ratio, southern elephant seal.

The inclusion of behavioral data in population models showed the strong influence that sex ratio has on the population viability of polygynous species (Gerber 2006). This framework allowed researchers to test suites of alternative hypotheses in conservation management, and to facilitate the identification of links between changes in social parameters (*e.g.*, group size, sex ratio, and mating behavior) and population viability.

We analyzed and applied a deterministic model to understand the relationship between social structure and the status of the southern elephant seal, *Mirounga leonina*, colony of Península Valdés (PV). The objective is to demonstrate that including the social structure improves the fit of population models to census data, and to provide a quantifiable effect of considering the social structure in this polygynous species. We focused on field surveys of harem size and adult sex ratios to describe social structure.

Elephant seals reproduce in harems that may vary in size from a few up to more than 100 females at peak breeding season (Laws 1956, Aarde 1980, Le Boeuf and Laws 1994). One male monopolizes control of the harem, although matings occur with males of lower status in the dominance hierarchy (Hoelzel *et al.* 1999). PV is a demographically isolated population that encompasses about 500 harems distributed along 200 km of open ocean coastline (Fig. 1). During the breeding season (September–October), most animals are located along the Atlantic front of PV, in a virtually uninterrupted distribution with harem distances that range less than 100 m to a few kilometers of empty but suitable beaches. Starting in the late 1960s, counts of this colony indicated that the core of the group was located to the north of the peninsula, in a stretch of about 120 km between Punta Buenos Aires and Punta Cantor. About 50 yr later, the colony expanded to the south and harems became much smaller in the north, with few or no peripheral males present in the smaller breeding groups and even some harems deserted by males. The opposite occurred in the south of PV, where harem size has been expanding (Campagna and Lewis 1992, Lewis *et al.* 1998). The only habitat difference between the northern and southern demographic subunits is that pebble beaches predominate in the north, while sandy substrates are typical of the south; however, both types of substrates intermingle in both coastal sections. To our knowledge, this dislocated demographic profile within the same colony, with no geographical barrier, has not been reported before and its population consequences have not been explored.

Long-term data for both demographic subunits of the PV colony of southern elephant seals are available on breeding population, social structure, and pup production (Campagna and Lewis 1992, Campagna *et al.* 1993). PV is unique for the species due to its sustained increase in pup production over the last several decades. Although it is unclear what factors led to the distributional shift within the colony, a descriptive model can be developed to address the spatially disjunctive social structure and demographics associated with the change. In fact, opportunity arises to study the interaction of these two, often-uncoupled aspects of species biology.

The specific objectives of the study were to: (1) develop a population model with social structure integrated as a variable in a fertility function, (2) apply the model to the entire colony and to the two demographic subunits with contrasting demographic profiles, and (3) test alternative parameter configurations to explain the decline in birth numbers in the north and the increase in the south.

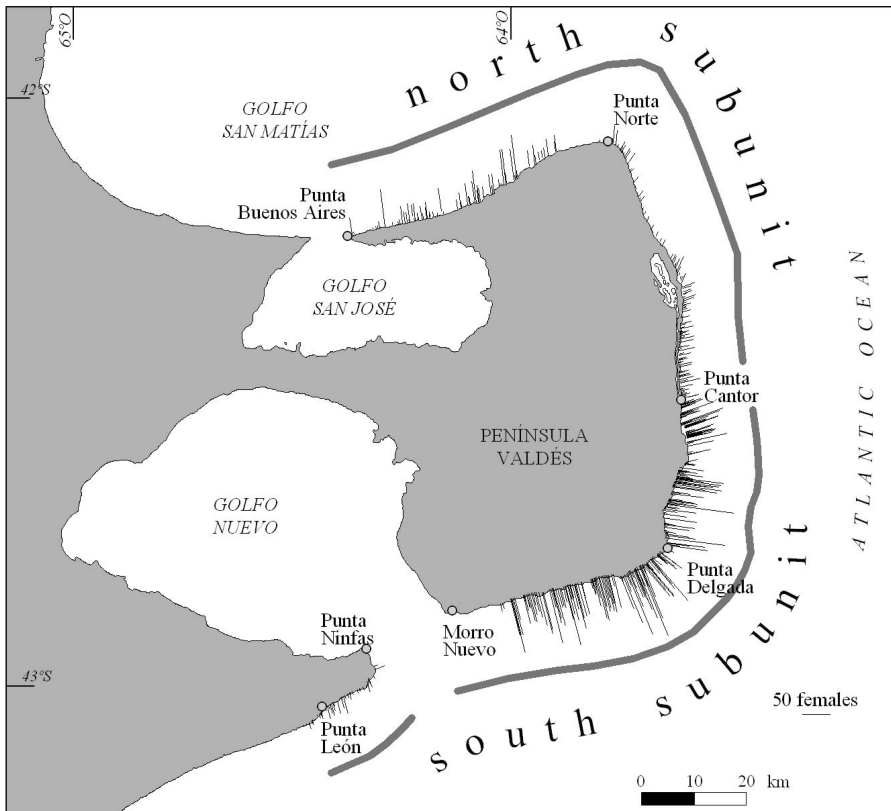


Figure 1. Distribution of seals at PV and nearby areas (subunit north and south indicated by the thick gray line following the contour of the coast). Thin lines provide an idea of harem sizes, length line is proportional to the number of females in the harem according to a scale given in the map. Harem location was georeferenced (GPS Garmin Rino 110) during the 2006 survey.

The most important southern elephant seal breeding colonies in the world, with the exception of PV, are distributed in subantarctic islands. The largest of all colonies, South Georgia, is characterized by seals dispersed along many beaches, some of which are located on islets, thus providing no real sense of an aggregation (Boyd *et al.* 1996). During the last century, several of the largest populations decreased in numbers (Hindell and Burton 1987; Guinet *et al.* 1992, 1999) with a few colonies being apparently stable (Boyd *et al.* 1996, Galimberti and Boitani 1999). In contrast, the size of the Patagonian colony of PV expanded and geographic barriers do not disrupt the distribution of animals. Census data are available for PV from 1969 to the present, but annually uninterrupted since 1995, contrasting with the paucity of data for other locations (Campagna and Lewis 1992, Campagna *et al.* 1993, Baldi *et al.* 1996, Lewis *et al.* 1998). An analysis of demographic patterns within PV may then provide insight to the problem of elucidating contrasting patterns in the distribution range of the species.

CENSUS DATA AND STUDY AREA

Annual terrestrial surveys of this colony have been conducted during the peak of the breeding season since 1995 (first week of October; Campagna and Lewis 1992, Campagna *et al.* 1993, Lewis *et al.* 1998). Surveys encompass the entire 200 km occupied by breeding seals at PV, and an additional 30–40 km of coastline to the south of PV where a few harems are found (Fig. 1). All animals were counted and assigned to easily differentiated age categories: suckling pups, weanling pups, adult females, subadult males, adult dominant males, and adult peripheral males. At the peak of the season, virtually all females ashore give birth to a pup and we found that the best estimate of the number of pups born is the sum of the number of adult females, weaned and dead pups (Boyd *et al.* 1996, Lewis *et al.* 2004). The annual mean harem size was defined as the average number of females per harem.

MODEL STRUCTURE

We defined the fertility function F , which is proportional to the female mating rate (proportion of females mated during the breeding season). We assessed the influence of the social structure by considering:

$$F(t) = (1 + R(t)^a)^{1/a} \quad (1)$$

$R(t)$ is a social structure variable evaluated from the observed sex ratio in the t breeding season and parameter a determines the strength of this variable on the function value. We considered two variants for R that differ according to whether only adult males ($R1$) or total males (adults plus subadults, $R2$) are included:

$$\begin{aligned} R1 &= \text{Mean harem size} \left(\frac{\text{Number of adult males}}{\text{Number of females}} \right), \\ R2 &= \text{Mean harem size} \left(\frac{\text{Total number of males}}{\text{Number of females}} \right). \end{aligned} \quad (2)$$

The fertility function corresponds to a generalized mean (Hardy *et al.* 1952, Caswell 2001) normalized such that $F(t)$ is bounded, $F(t) \leq 1$, for $a < 0$. Also, $F(t) = \text{Min}(1, R(t))$ when a is tending to $-\infty$. Using the observed values for variable $R(t)$ (from Eq. (2), where $1 < R1, R2 < 5.5$) and elementary properties of generalized means (Hardy *et al.* 1952), we used the parameter a to quantify the influence of social structure, anywhere between strong (a tending to 0) to null (a tending to $-\infty$; *i.e.*, linear model with $F(t) = 1$). The parameter a is related to the elasticity of F with respect to R , that is the proportional response of F to a proportional change in R . In fact, the elasticity of F with respect to R is defined as

$$\frac{R}{F} \frac{\partial F}{\partial R} = \frac{R^a}{1 + R^a}, \quad (3)$$

which is an increasing function of a (assuming $R > 1$).

We used a stage-based model, corresponding to the life cycle of the female southern elephant seal, to represent population dynamics. We developed two versions of the

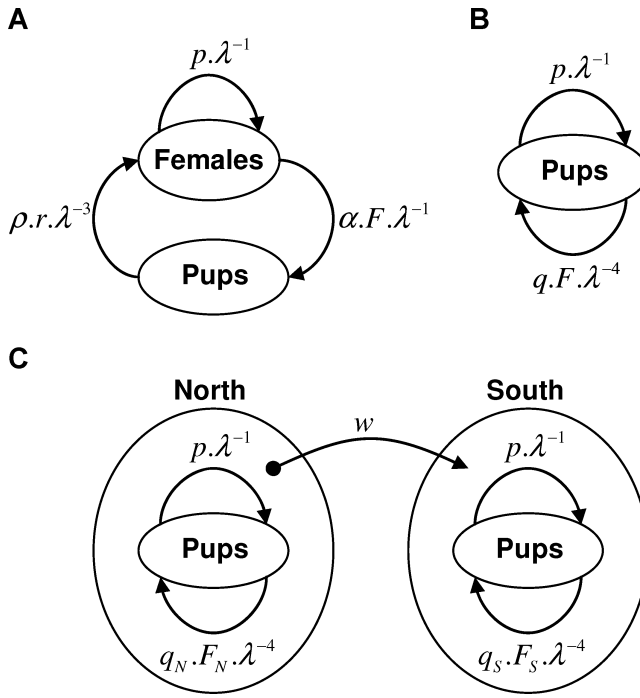


Figure 2. Life cycle graph for the considered models. Notation corresponds to a z -transformed graph where exponents on λ indicate the time interval, in years, required for the transition (Caswell 2001). (A) Basic aggregated model with two stages. (B) Reduced aggregated model with a single stage, applied to the entire population of PV as a single unit. (C) Two-demographic subunit model with unit-specific recruitment parameters (q_N , q_S) and a proportion of one-way migrating females (w).

model, with different levels of population structure. A basic, aggregated model was developed to represent the dynamics of the entire population as a single unit. We first considered two stages (Fig. 2A): females (adult females 3-yr old and older) and pups (newborn individuals of both sexes). A system of two equations for the number of pups (N) and the number of females (N_f) describes this model:

$$\begin{aligned} N(t) &= \alpha F(t-1)N_f(t-1) \\ N_f(t) &= \rho r N(t-3) + p N_f(t-1), \end{aligned} \tag{4}$$

where t represents the breeding season, ρ the proportion of females at birth, r the recruitment rate of adult females, p the adult female survival, and α a fertility constant. Because we do not have an independent estimation of the total number of females, we reduced the aggregated model to one with a single stage (Fig. 2B), which collapses Equation (4) to a single equation:

$$N(t) = q F(t-1)N(t-4) + p \frac{F(t-1)}{F(t-2)} N(t-1). \tag{5}$$

Because ρ , r , and α in Equation (4) cannot be estimated independently, we defined a composite recruitment parameter $q = \rho r \alpha$. Parameters q , p , and α from the fertility function were estimated by fitting the model to observed data (see below).

We developed a second, more complex version of the model to accommodate the influence of population subdivision. The differences in pup production between the north and the south subunits [$N_N(t)$ and $N_S(t)$] were modeled by considering unit-specific recruitment parameters (q_N , q_S) and a proportion of females migrating from north to south (w , Fig. 2C). The equations for the two-demographic subunit model were:

$$\begin{aligned} N_N(t) &= (1 - w) \left[q_N F_N(t - 1) N_N(t - 4) + p \frac{F_N(t - 1)}{F_N(t - 2)} N_N(t - 1) \right] \\ N_S(t) &= q_S F_S(t - 1) N_S(t - 4) + p \frac{F_S(t - 1)}{F_S(t - 2)} N_S(t - 1) \\ &\quad + w \left[q_S F_S(t - 1) N_N(t - 4) + p \frac{q_S}{q_N} \frac{F_S(t - 1)}{F_N(t - 2)} N_N(t - 1) \right] \end{aligned} \quad (6)$$

MODEL FIT AND MODEL COMPARISONS

We set the adult survival to $p = 0.842$, based on previous estimates from mark-recapture data (Pistorius *et al.* 2004). Hence, two free parameters remain for the aggregated population model (a , q), and four for the two-subunit model (a , q_N , q_S , w). To estimate these parameters, the model was projected for each year in the period 1999–2006, as a function of the previous year's counts and pup counts from 4 yr earlier. Given model projections, $N(t)$, and pup counts from surveys, $O(t)$, maximum likelihood parameter estimates were obtained by minimizing:

$$S = \frac{1}{\sigma^2} \sum_{1999}^{2006} (\ln O(t) - \ln N(t))^2. \quad (7)$$

For the two-demographic subunit model, the projections $N_N(t)$ and $N_S(t)$ were matched with the observed values in each area fitting Equation (7) as a double summation. The estimation method corresponds to a maximum likelihood estimation assuming a likelihood function Lik with lognormal process error, where $S = -2 \ln(Lik)$ (Hilborn and Mangel 1997). Parameter σ^2 represents the error variance and was estimated by the residual variance corrected by the number of observations ($n = 8$ for the aggregated population model and $n = 16$ for the two-demographic subunit model). In order to test the support provided by the data to non-constant fertility function (*i.e.*, fertility dependence on social structure), maximum likelihood models were tested against their linear reduction version (constant per capita fertility, $a = -1,000$) by means of a likelihood ratio test (Hilborn and Mangel 1997, Table 1).

The role of recruitment and migration in the dynamics of the subunits was tested with three basic reductions of the two-demographic subunit model, by adding restrictions in specific parameters: Equal Recruitment ($q_N = q_S$), No Migration ($w = 0$), and Linearity ($a = -1,000$). The eight alternative models defined by all combination of these reductions (Table 2) were compared using their maximum likelihood estimates S value, likelihood ratio test for nested models,

Table 1. Fitting the aggregated and the two-demographic subunit (*) models to census data, with alternatives social variables (R1 and R2). General models were compared with its linear reductions ($a = -1,000$) using the maximum likelihood estimates S value and a likelihood ratio test (Hilborn and Mangel 1997). The error variance (σ^2) was estimated, in each case, from general model residual variance taking into account the number of observations (n).

Social variable	S value			σ^2	Linear vs. General	
	General model	Linear reduction	n		(χ^2_1)	P -value
R1	3.767	3.767	8	0.0014	0	1
R2	4.224	5.273	8	0.001	1.049	0.306
R1 (*)	13.012	13.245	16	0.0035	0.233	0.629
R2 (*)	12.893	16.920	16	0.0027	4.027	0.045

and Akaike Information Criterion (AIC, Hilborn and Mangel 1997). The $AIC = 2k - 2 \cdot \ln(Lik)$, where k is the number of free model parameters, thus in this case $AIC = 2k + S$.

The number of births for the entire PV population grew steadily in the last 11 yr (from 12,430 pups in 1995 to 14,350 in 2006, Fig. 3). For the same period, the north demographic subunit declined from 3,530 to 3,070 pups, whereas the south subunit increased from 8,900 to 11,280 pups (Fig. 3). Both variables of social structure (R1 and R2) captured differences between subunits (Fig. 3). R1 ranged from 1.03 to 1.54 in the north and from 2.05 to 3 in the south, whereas R2 ranged from 1.95 to 2.87 in the north and from 4.38 to 5.41 in the south.

The models with social structure variable R1 fitted census counts as a linear standard model (Table 1). The two-demographic subunit model with social structure variable R2 showed the strongest differences with the linear model ($\chi^2_1 = 4.027$, $P < 0.05$; Table 1). The parameter $a = -1.131$ quantified the influence of the social structure on the number of births in the following season with a restricted 95% confidence interval (-5.885 to -0.399). Annual values for the fertility function ranged from 0.71 to 0.79 in the north and from 0.86 to 0.88 in the south (15% lower in the north). Recruitment was similar in the two subunits: $q_N = q_S = 0.209$ (0.136–0.5) and the proportion of migrating females was $w = 0.014$ (0–0.059). The projected growth rates for the stage based model with social structure were $\lambda_N = 0.99$ in the north and $\lambda_S = 1.02$ in the south. The growth rate of the linear aggregated model was $\lambda = 1.01$.

The most parsimonious model to explain the differences between the two subunits was one with equal recruitment, without migration, and with social structure effects on fertility (Table 2). The estimates were $a = -0.928$ and $q = 0.225$. AIC indicated that the next best model was one with equal recruitment and migration; however, for that model the estimates of a , q , and w matched that of the general model.

The likelihood ratio test for nested models showed that the linear model always was rejected as reduction of the others (Equal Recruitment, No Migration and Linear vs. Equal Recruitment, No Migration: $\chi^2_1 = 6.388$; Equal Recruitment and Linear vs. Equal Recruitment: $\chi^2_1 = 4.027$; No Migration and Linear vs. No Migration: $\chi^2_1 = 4.208$; $P < 0.05$ in all the cases).

Table 2. Testing effect of different combinations of migration and recruitment in the two-demographic subunit model with R2 social variable. (a) The potentiality of the fit was assessed by the maximum likelihood estimates S value, and by the Akaike Information Criterion (AIC). (b) Maximum likelihood parameter estimates and 95% confidence interval (from likelihood profiles) for the three most parsimonious models.

(a)		(b)			
Model	Restrictions	S	AIC	Delta AIC	Akaike weight
1. General		12.893	20.893	3.582	0.066
2. Equal Recruitment	$q_N = q_S$	12.893	18.893	1.582	0.181
3. Equal Recruitment, No Migration	$q_N = q_S, w = 0$	13.311	17.311	—	0.400
4. Equal Recruitment, No Migration, and Linear	$q_N = q_S, w = 0, a = -1,000$	19.699	21.699	4.388	0.044
5. Equal Recruitment and Linear	$q_N = q_S, a = 1,000$	16.920	20.920	3.609	0.066
6. No Migration	$w = 0$	13.082	19.082	1.771	0.165
7. No Migration and Linear	$w = 0, a = -1,000$	17.291	21.291	3.980	0.054
8. Linear	$a = -1,000$	16.920	22.920	5.609	0.024

Model	Parameters			
	a	q_N	q_S	w
3.	-0.928 (-2.750-0.399)	0.225 (0.155-0.5)	0.225 (0.155-0.5)	0
2.	-1.131 (-5.885-0.39)	0.209 (0.155-0.5)	0.209 (0.155-0.5)	0.014 (0-0.059)
6.	-1.083 (-5.025-0.391)	0.198 (0.126-0.5)	0.217 (0.156-0.5)	0

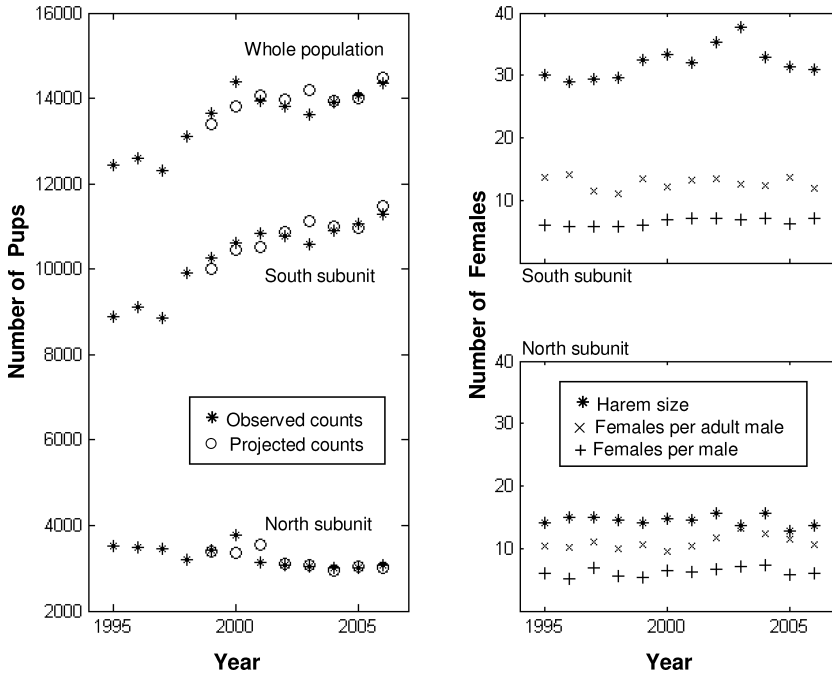


Figure 3. Left box: Pup counts for the whole PV population and the two demographic subunits. The two-demographic subunit model, with social variable R_2 , projections from 1999 to 2006 are included as a graphical representation of the fit. Right boxes: Social structure for the two subunits represented by annual mean harem size, mean number of females per adult male, and mean number of females per male (adults plus subadults).

CONCLUSIONS

The integration of social structure data (sex ratio and harem size) into a simple population model of the southern elephant seal colony of PV improved the interpretation of census data for the divergent demographic trends between north and south colony subunits. We used parameters easily obtained in the field and a generalized mean type fertility function to quantify the influence of social structure on the number of pups.

Birth and fertility functions are essential components of two-sex models (Caswell 2001). These models provide a framework to develop more general and predictive perspectives that integrate social elements of the mating system (Gerber 2006). Generalized mean functions are commonly used to describe marriage, birth, and fertility functions in human demography and population dynamics (Pollard 1997, Caswell 2001, Legendre *et al.* 1999, Bessa-Gomes *et al.* 2004, Gerber 2006). The more commonly used mean functions are the minimum function (a tending to $-\infty$, Legendre *et al.* 1999, Bessa-Gomes *et al.* 2004) and the harmonic mean ($a = -1$, Pollard 1997, Gerber 2006). Selecting a particular mean function requires the assumption of a particular shape for the response of the fertility function to changes in the operational sex ratio and social structure. In this work, we did not select a particular mean function and we estimated the value of a . The estimated value

($a = -1.131$) is similar to the harmonic mean, but our approach provided a range for the "fertility function shape" (95% confidence interval, -5.885 to -0.399). Results suggest the need for further data on the fertility function shape and its implication for population dynamics of polygynous marine mammals.

Contrasting a fertility function with field measures is difficult due to limited variability in the sex ratios (Caswell 2001). Despite an increase in the annual number of births at PV, the adult sex ratio remained similar for the same period in the entire colony, ranging between 0.138 and 0.177 from 1995 to 2006. It is in this context that the two subunits provided a scenario to assess the influence of the social structure on population dynamics, as differences between north and south allowed us to estimate the fertility function. The number of females per male is similar at both sites, but harem size differs greatly (Fig. 3). We regularly observe harems without males during censuses of the northern PV subunit. While it is possible that additional dominant males arrive later in the season, our results suggest that the presence of these female-only groups is associated with fewer births in the next year.

From the tested alternative hypotheses, the model with equal recruitment and without migration provided the most parsimonious explanation for the divergent demographic profiles found within the same colony. Mark-recapture studies of tagged individuals showed that most seals remain within 50 km of their tagging sites, and resights support strong adult female site fidelity for breeding areas (Lewis *et al.* 1996). Low recruitment in the North subunit due to high juvenile mortality cannot however be ruled out. Attacks on seals by killer whales is more commonly observed in the north side of PV (López and López 1985), but the relative low frequency of occurrence suggests that it may not be a significant contributor to the observed seal decline in the sector.

Population declines are more commonly linked to variables that affect survival (lack of space, lack of food, disturbance, pollution, or other threats to population viability) (Gerber *et al.* 2004). However, none of the listed variables would be relevant for PV, where the conditions favor population increase (Campagna and Lewis 1992, Lewis *et al.* 1998).

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, Guinet *et al.* 1992, 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 for some of these population changes remain unknown (McMahon *et al.* 2005). A lack of males was proposed as a cause of population decline in Marion Island (Skinner and van Aarde 1983). This hypothesis was tested by looking at the sexual activity and other social and behavioral variables during three breeding seasons, and later was rejected (Wilkinson and van Aarde 1999). However, a possible interdependence of social structure and demography on a longer temporal scale was not tested, and our model could be a tool for comparative studies between populations of different trend. The approach of this study can be applied to analyze the relation between social structure and population dynamics when the following conditions occur: (1) long-term time-series in number of pups born are available, (2) counts are favored by synchronized and predictable haul-out sites, (3) harem size and adult sex ratios can be recorded, and (4) some population parameters of recruitment and survival are known.

More generally, this approach may be used to identify the relative effect of alternative scenarios or management strategies on population growth of other mammals, when there is evidence that social structure may be playing a significant role.

Milner-Gulland *et al.* (2003) have reported a drastic decline in female fertility due to an extremely skewed sex ratio in the saiga antelope (*Saiga tatarica tatarica*), a critically endangered harem-breeding ungulate. They described a threshold-type fertility function (Milner-Gulland *et al.* 2003) which corresponds to a small value for the parameter a in the generalized mean family. In such a case, the consideration of a model incorporating social structure parameters could help in the design and evaluation of management strategies. Ultimately, the integration of social and demographic data helps to identify which practical observations are most important (Gerber 2006), improving the available techniques for monitoring natural populations of southern elephant seals.

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LITERATURE CITED

- AARDE, R. J. VAN. 1980. Harem structure of the southern elephant seal *Mirounga leonina* at Kerguelen Island. *Revue d'Ecologie: La Terre et la Vie* 34:41–44.
- BALDI, R., C. CAMPAGNA, S. PEDRAZA AND B. J. LE BOEUF. 1996. Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. *Animal Behaviour* 51:717–724.
- BESSA-GOMES, C., S. LEGENDRE AND J. COLBERT. 2004. Allee effects, Mating systems and the extinction risk in populations with two sexes. *Ecology Letters* 7:802–812.
- BOYD, I. L., T. R. WALKER AND J. PONCET. 1996. Status of southern elephant seals at South Georgia. *Antarctic Science* 8:237–244.
- CAMPAGNA, C., AND M. N. LEWIS. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science* 8:387–396.
- CAMPAGNA, C., M. N. LEWIS AND R. BALDI. 1993. Breeding biology of southern elephant seals in Patagonia. *Marine Mammal Science* 9:34–47.
- CASWELL, H. 2001. *Matrix population models*. 2nd edition. Sinauer Associates, Inc., Sunderland, MA.
- GALIMBERTI, F., AND L. BOITANI. 1999. Demography and breeding biology of a small, localized population of southern elephant seals (*Mirounga leonina*). *Marine Mammal Science* 15:159–178.
- GERBER, L. R. 2006. Including behavioral data in demographic models improves estimates of population viability. *Frontiers in Ecology and the Environment* 4:419–427.
- GERBER, L. R., M. T. TIMKER, D. F. DOAK, J. A. ESTES AND D. A. JESSUP. 2004. Mortality sensitivity in life-stage simulation analysis: A case study of southern sea otters. *Ecological Applications* 14:1554–1565.
- GUINET, C., P. JOUVENTIN AND H. WEIMERSKIRCH. 1992. Population changes, movements of southern elephant seals on Crozet and Kerguelen Archipelagos in the last decades. *Polar Biology* 12:349–356.
- GUINET, C., P. JOUVENTIN AND H. WEIMERSKIRCH. 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.
- HARDY, G. H., J. E. LITTLEWOOD AND G. POLYA. 1952. *Inequalities*. Cambridge University Press, Cambridge, U.K.

- HILBORN, R., AND M. MANGEL. 1997. The ecological detective: Confronting models with data. Princeton University Press, Princeton, NJ.
- HINDELL, M. A., AND H. R. BURTON. 1987. Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *Journal of Zoology* 213:365–380.
- HOELZEL, R. A., B. J. LE BOEUF, J. REITER AND C. CAMPAGNA. 1999. Alpha male paternity in elephant seals. *Behavioral Ecology and Sociobiology* 46:298–306.
- LAWS, R. M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. Falkland Islands Dependencies Survey. Scientific Report (London), No. 13. 87 pp.
- LE BOEUF, B. J., AND R. M. LAWS. 1994. Elephant seals: An introduction to the genus. Pages 1–26 in B. J. Le Boeuf and R. M. Laws, eds. *Elephant seals: Population ecology, behavior and physiology*. University of California Press, Berkeley, CA.
- LEGENDRE, S., J. COLBERT, A. P. MØLLER AND G. SORCI. 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., C. CAMPAGNA AND F. QUINTANA. 1996. Site fidelity and dispersion of southern elephant seals from Patagonia. *Marine Mammal Science* 12:138–147.
- LEWIS, M. N., C. CAMPAGNA, F. QUINTANA AND V. FALABELLA. 1998. Estado actual y distribución de la población del elefante marino del sur en la Península Valdés, Argentina. *Mastozoología Neotropical* 5:29–40.
- LEWIS, M. N., C. CAMPAGNA AND J. ZAVATTI. 2004. Annual cycle and inter-annual variation in the haul-out pattern of a growing southern elephant seal colony. *Antarctic Science* 16:219–226.
- LÓPEZ, J. C., AND D. LÓPEZ. 1985. Killer whales (*Orcinus orca*) of Patagonia and their behavior of intentional stranding while hunting near shore. *Journal of Mammalogy* 66:181–183.
- MCMAHON, C. R., M. N. BESTER, H. R. BURTON, M. A. HINDELL AND C. J. A. BRADSHAW. 2005. Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Review* 35:82–100.
- MILNER-GULLAND, E. J., O. M. BUKREEVA, T. COULSON, A. A. LUSHCHEKINA, M. V. KHOLODOVA, A. B. BEKENOV AND I. A. GRACHEV. 2003. Reproductive collapse in saiga antelope harems. *Nature* 422:135.
- PISTORIUS, P. A., M. N. BESTER, M. N. LEWIS, F. E. TAYLOR AND C. CAMPAGNA. 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* 26:11–24.
- SKINNER, J. D., AND R. J. VAN AARDE. 1983. Observations on the trend of the breeding population of southern elephant seals, *Mirounga leonina*, at Marion Island. *Journal of Applied Ecology* 20:707–712.
- WILKINSON, I. S., AND R. J. VAN AARDE. 1999. Marion Island elephant seals: The paucity of males hypothesis tested. *Canadian Journal of Zoology* 77:1547–1554.

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