BREEDING BIOLOGY OF SOUTHERN ELEPHANT SEALS IN PATAGONIA

C. CAMPAGNA,[1,2] M. LEWIS,[1] R. BALDI[3]

[1]Centro Nacional Patagónico, 9120 Puerto Madryn, Chubut, Argentina
[2]Wildlife Conservation International, New York Zoological Society, Bronx Zoo,
Bronx, New York, New York 10460
[3]Universidad Nacional de la Patagonia, 9120 Puerto Madryn, Chubut, Argentina

ABSTRACT

Elephant seals breed in Patagonia (Península Valdés, Argentina) from late August to early November, reaching peak numbers during the first week in October. Observations of this population over the past ten years yielded similar results. Eighty percent of the pups were born by 2 October. Most (96%) of 663 females marked during three breeding seasons gave birth to a pup. Females stayed on land a mean of 28 d, gave birth 6 d after arrival, nursed their pups for 22 d, and copulated a mean of 2.5 times 20 d after parturition and 2 d before departure. Copulations peaked during the third week in October. Males spent 57–80 d on land fasting and defending harems of up to 134 females (median 11–13 females, depending on year). Most (96%) marked females that gave birth (n = 636) also weaned their pups successfully. Pup sex ratio was unity. Harems were smaller and breeding occurred about three weeks earlier in Patagonia than in other colonies. Thermal conditions, day length and food availability may explain clines in the timing of breeding events between populations. Other parameters of the breeding season for the expanding Patagonia colony are similar to those for declining southern elephant seal populations elsewhere.

Key words: southern elephant seal, *Mirounga leonina,* Patagonia, breeding behavior.

Southern elephant seals, *Mirounga leonina,* have a circumpolar breeding and molting distribution on both sides of the Antarctic Convergence (McCann 1985). Several of the largest populations of this species have declined sharply in the past 50 years (Hindell 1990, 1991). The reasons for these declines are unclear and there is an urgent need to report information on the biology of the species on land and at sea to help identify factors causing declines in numbers. This paper provides an account of the breeding biology of southern elephant seals at Península Valdés, in the Argentine Patagonia, one of the least known populations of one of the best studied phocids.

Adult southern elephant seals have two pelagic and two terrestrial phases in their annual cycle (Laws 1956*a*, 1960; Carrick *et al.* 1962*a*, *b*). Seals come ashore to breed (August–November) and molt (December–February). The rest of the year is spent at sea. At the onset of the breeding season, males aggressively establish a dominance hierarchy. Females are gregarious and give birth to a single pup in harems reproductively controlled by large, adult alpha males. About three weeks after birth, females wean their pups, mate and return to sea. Two months later females haul out again for about one month to molt their skin. After the molt, a long pelagic period precedes the subsequent breeding season.

The Valdés colony has distinctive ecological, demographical and geographical features. It is apparently the only one in the world that is growing (Vergani *et al.* 1987, Campagna and Lewis 1992). About 9,000 pups are born in Patagonia every year, and pup production has been increasing at a rate of 6% per year since the late 1960s (Campagna and Lewis 1992). Besides the small colony at Gough Island (Bester 1980), the one in Patagonia is the northernmost large true seal breeding population in the Southern Hemisphere. It is located on a continent rather than on an island, and in temperate rather than antarctic or subantarctic waters. It faces a 550 km-broad continental shelf where marine productivity is high, and fish and squid stocks abundant (Bellisio *et al.* 1979, Anonymous FAO report 1991). Animals are widely distributed along 200 km of coastline, harems are small relative to other populations and pup mortality is low compared to its northern counterpart (Le Boeuf and Petrinovich 1974, Honigman 1988, Lewis 1989). The Valdés population has never been affected by intensive sealing, unlike all other major breeding sites of the species (Laws 1960, van Aarde 1980*a*, Hindell and Burton 1988).

Information on the biology of *M. leonina* at Península Valdés comes from a variety of studies. The colony was first described in the late 1940s (Carrara 1952) and basics of its population dynamics and breeding behavior were reported afterwards (Daciuk 1973, 1974; Le Boeuf and Petrinovich 1974; Scolaro 1976; Vergani 1985; Honigman 1988; Lewis 1989). Although these studies provide valuable descriptions of the breeding biology of the species, detailed information is lacking on daily changes in numbers of animals on the beach during the breeding season, social structure of the rookery and reproductive behavior of both sexes during several breeding years.

This paper updates and expands on previous reports, attempting to fill the lack of precision in our knowledge of the annual cycle of elephant seals in Patagonia. It presents the daily variation in numbers of males, females and pups, describes in detail the time of reproductive events and provides data on pup mortality, sex ratio, harem size and male and female reproductive behavior.

METHODS

Península Valdés (42°30'S, 64°W) is located in Patagonia, southern Argentina (Fig. 1). At Península Valdés elephant seals occupy a 200-km stretch of coastline, from Punta Buenos Aires to Punta León (Fig. 1; Lewis 1989, Campagna and
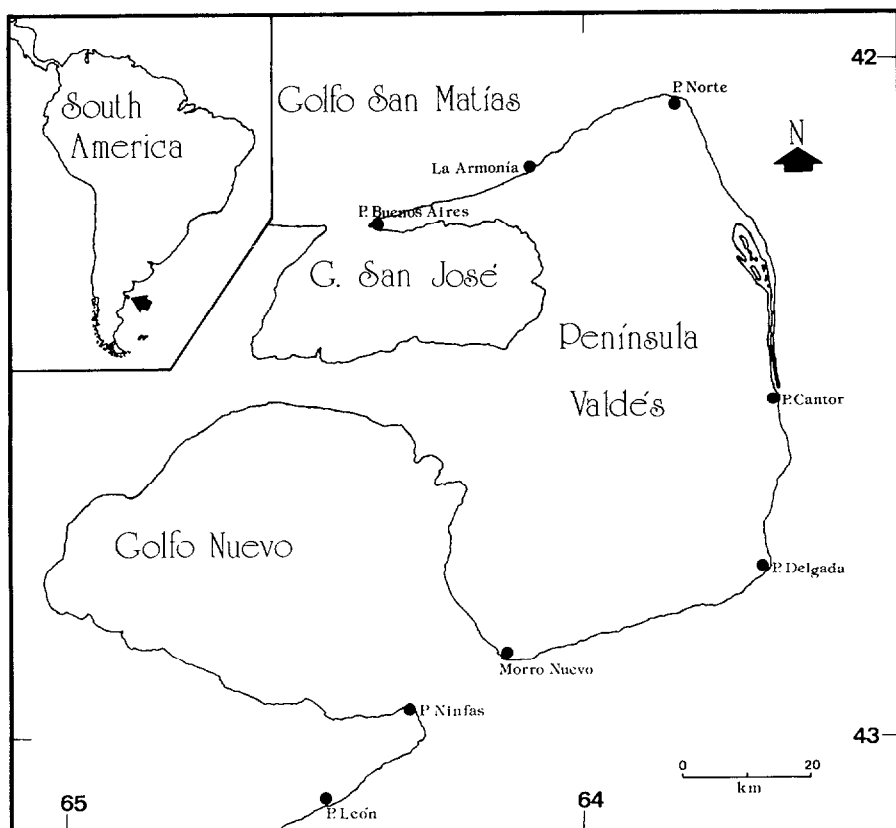
Figure 1. Geographic location of the study area.

Lewis 1992). Most breeding beaches are spacious and have a pebble or sandy substrate (Le Boeuf and Petrinovich 1974, Campagna and Lewis 1992).

Data were collected during three complete reproductive seasons (mid-August to early November, 1988, 1990 and 1991) at La Armonia beach (1988) and at Punta Delgada (Fig. 1). Additional data were gathered at Punta Norte (August–October, 1982) and opportunistically at different places along the coastline of the Península each year, from 1981 to 1991 (Lewis 1989). Basic breeding parameters were illustrated with data from La Armonia.

Aerial censuses were conducted at the peak of the 1982 (1 October), 1989 (7 October) and 1990 (4 October) reproductive seasons (Campagna and Lewis 1992), when about 96% of the breeding individuals are expected to be ashore (Lewis 1989). All harems larger than 10 females were photographed. Solitary individuals, mating pairs (breeding groups of one male and one female), and small harems (less than 10 females) were recorded. Seals in each photograph were counted and categorized as breeding females, breeding males (harem bulls and challengers), pups, and weanlings. From these counts, we calculated total number of breeding groups and median harem size. Breeding groups include

harems and mating pairs. A harem was defined as a group of two or more females with an alpha bull in attendance. The external two rows of females of some large harems (>50 females) were considered peripheral. The rest were central. Central females were closer to harem bulls. Bachelors or challengers were adult males peripheral to the harems.

Daily counts of the study areas were conducted on foot, differentiating alpha bulls, challengers, adult females with and without pups, pups and weanlings. Dead pups were counted and removed from the beach. Peak season was the time with maximum number of females ashore. The length of the breeding season was estimated from the arrival of the first bulls until the last pup was weaned. The sex of newly weaned pups was determined at the end of the 1984, 1988, and 1989 seasons.

As fully grown females and males arrived at the breeding place, a readily visible name was printed on each side of the animal with a black dye or a bleaching agent (Le Boeuf and Peterson 1969). Identification cards and a serial record were kept during daylight hours of the presence and key activities of marked seals to calculate occurrence and intervals between reproductive events (arrival-parturition-copulation-weaning-departure). Although copulations occur at night (Campagna, unpublished information), we did not conduct regular observations at this time of the day. Thus, our mating data only reflect observed daytime copulations.

The length of the day at different latitudes was determined by the time of sunrise and sunset according to the equation $\cos h = -\tan \delta \cdot \tan \phi$, where δ is declination and ϕ is latitude (Liou 1980).

Averages are given as means $\pm$ one standard deviation (SD) unless stated otherwise.

RESULTS

Breeding cycle—The first adult males and females hauled out during the third week of August (Fig. 2). The number of males increased in early September and remained high during the following eight weeks. Males involved in reproduction arrived at the breeding area in late August and early September. Except for small harems (2–5 females) and mating pairs, alpha males were established in their harems by the second week of September. Only one of 13 marked males that were the alpha male of large harems (>50 females) in mid-September had been displaced by newcomers later in the season. Most harem masters abandoned the beaches by mid-November, after all the females had been mated. Estimated tenure in the breeding area for 11 dominant males was 67 ± 8 d (range = 57–80 d), *vs.* 51 ± 9 d (range = 31–71 d) for 27 bachelor males (t-test between the means = 4.9; df = 36; $P < 0.05$).

The numbers of females increased steadily from early September onwards, peaked during the period 1–5 October, remained high for one week and declined from early October until the end of the season (Fig. 2). The number of females on land at peak season represented 96% of the females that reproduced in one year; only four percent of the females arrived after 6 October. The last pregnant
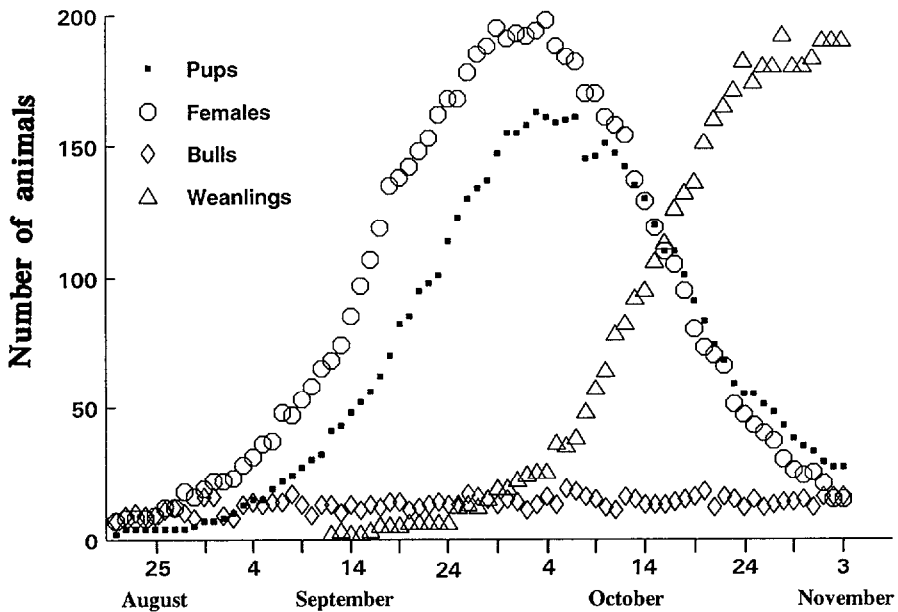
Figure 2. Number of adult females, males, pups and weanlings as a function of date during the breeding season. Data for the 1988 breeding season.

female came ashore to give birth on 25 October. The duration of the breeding season was 75–80 d. The adult sex ratio was moderately but not significantly female biased early (1:1.6; χ^2 = 1.5; P > 0.05; n = 30) and late (1:1.6; χ^2 = 0.6; P > 0.05; n = 37) in the season, and highly female biased at peak season (1:13.6), when about 210 animals were breeding (Fig. 3).

Most females mated inside harems. From a range of 420–487 mating associations, depending on the year, 91–93% were within harems and 7–9% were mating pairs composed of one male and one female. About 0.4% of the females gave birth in isolation from other seals. Median harem size at peak season and for the entire Península varied from 11–13 females, depending on the year (n = 381–445). The largest harem had 134 females at peak season.

Parturitions—Most females that came ashore were pregnant (96% of 663 marked animals). Parturitions occurred a mean of 5.7 days (SD = 1.9, n = 37) after arrival at the rookery. The first births were recorded in late August and continued up to 30 October, with numbers of births peaking in late September (Fig. 4). Afterwards, the number of pups at the beach remained almost constant for one week and declined thereafter (Fig. 2). Sixty percent of the births occurred from 8–28 September, and 80% of the pups were born by 2 October. Pups counted on the beach at the peak of the pupping season represented about 70% of the pups born.

Significantly more cows gave birth at dusk or at night. Of 69 females observed in 1988, 50 (73%) gave birth between 1800 and 0800 (χ^2 = 13.9, df = 1, P < 0.05). Fifty-five percent of 29 births occurred in the breach position, the
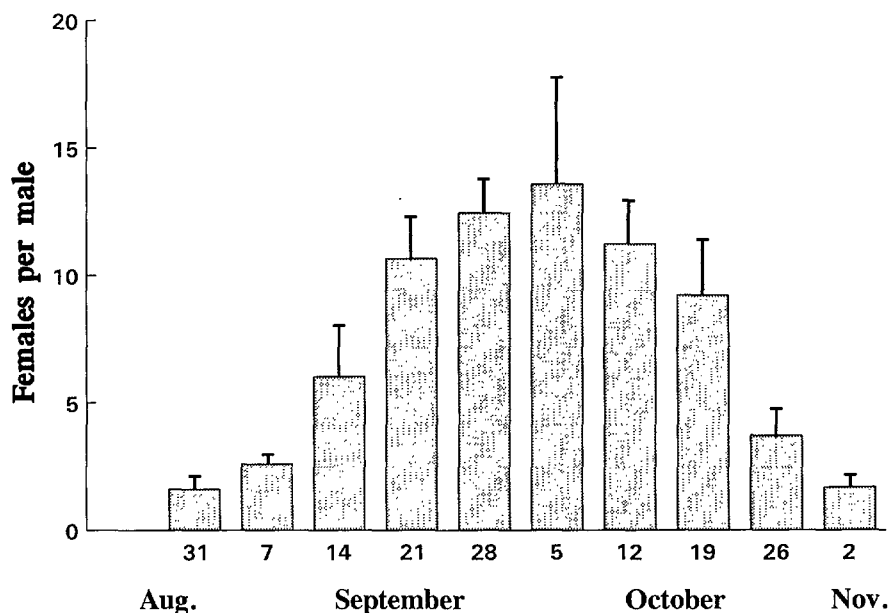
Figure 3. Weekly variation in adult sex ratio (expressed as females : males) during the 1988 breeding season.

rest (45%) were cephalic ($\chi^2 = 0.31$, df = 1, $P > 0.05$). There was a slight preference to give birth in the periphery of the harems. Of 29 births, 69% occurred in the periphery and 31% in the center of the harem ($\chi^2 = 4.2$, df = 1, $P < 0.05$), despite the fact that about 50% of the females were peripheral.

Copulations—The first copulations occurred during the second week of September and continued until the last female left in early November (Fig. 5). Every year, mating frequency reached a peak during the second and third week in October. A second peak of copulations was observed only at La Armonia during the 1988 breeding season, when only a few females remained at the breeding beach and two males copulated with them on many occasions (Fig. 5).

Harem masters were involved in 65% of 361 copulations by 135 females. The rest of the matings (35%) took place with subordinate males. Of 135 marked females, 54% copulated only with alpha males, 20% only with subordinate males, and 26% with both.

Females copulated a mean of 20.3 d after parturition (SD = 2.1, $n = 51$). Most females copulated several times during the breeding season. Of 135 females seen copulating 362 times during daylight hours, 32% copulated once and 68% copulated on two or more occasions (Fig. 6). Females were observed copulating a mean of 2.5 times during the breeding season (SD = 1.9; range = 1–9; $n = 133$) within a mean period of 2.5 d (SD = 1.1, range = 1–5 d, $n = 39$ females). Three females not included in this sample copulated 11, 15 and 16 times with at least three different males during a period of 20 daylight hours.
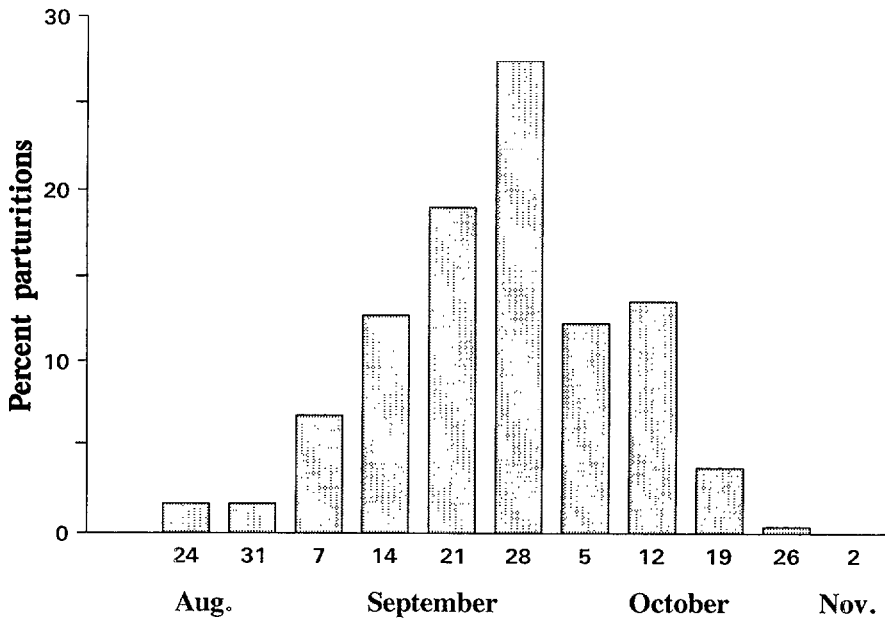
Figure 4.   Distribution of parturitions (as percentage of 237 births) as a function of date during the breeding season.
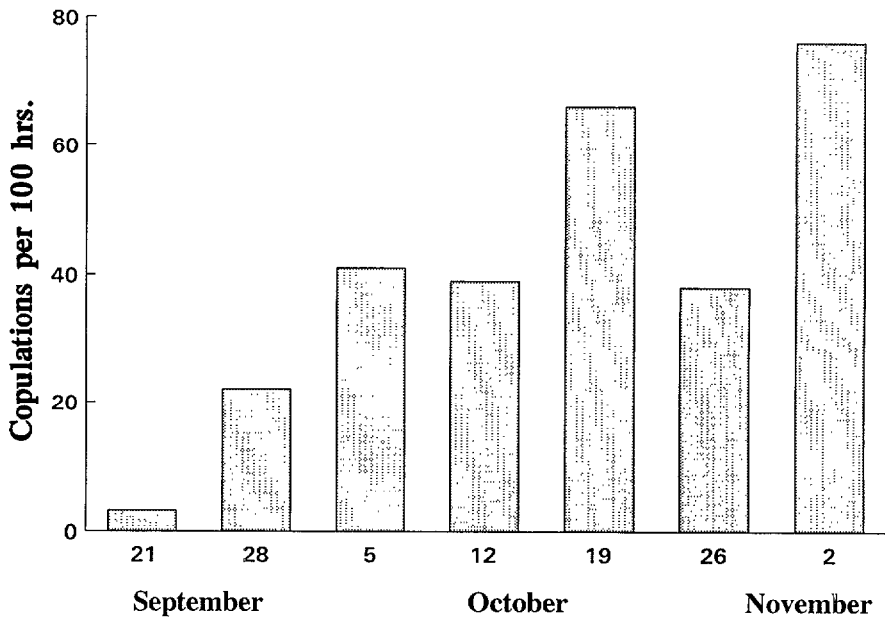

Figure 5.   Distribution of daylight copulations of six males as a function of date during the breeding season (data from La Armonia beach).
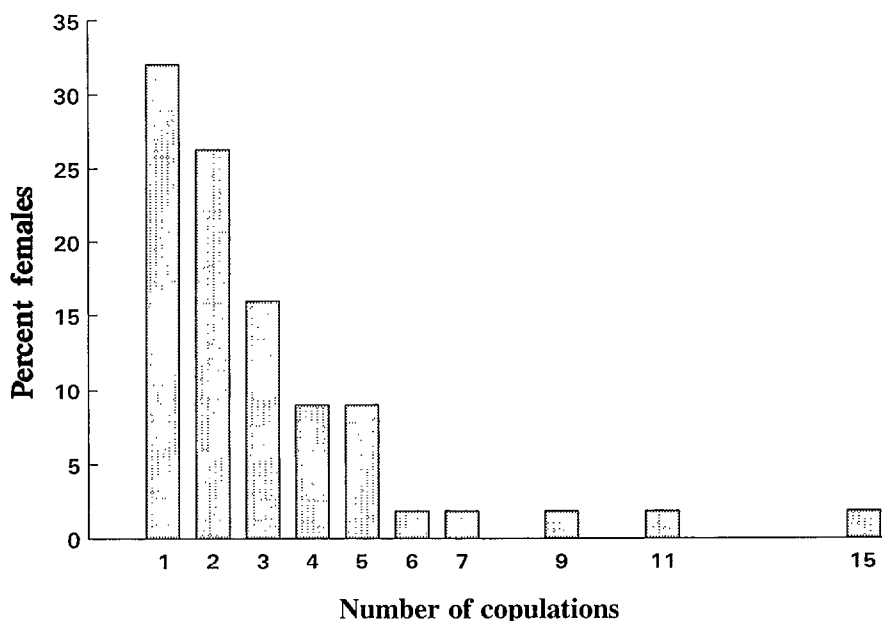
Figure 6.   Frequency distribution of number of copulations per female.

Of 88 females that copulated more than once, 49% mated only with one male. The remaining 51% copulated with 2–5 different males (mean ± SD; 2.5 ± 0.8). Of 57 marked females observed since early stages of their estrus, 88% copulated for the first time with an alpha male. The remaining 12% first copulated with peripheral males.

The rate at which copulations occurred did not vary as a function of time of the day. Of 362 copulations, 34% occurred from 0900 to 1200, 36% from 1201 to 1500, and 30% from 1501 to 1800 (χ^2 = 1.9, df = 2, P < 0.05).

Weaning and pup mortality—Most females weaned their pup successfully (96% of 636 animals) 22.4 d after birth (SD = 1.7, range = 16–26 d, n = 215). The first pups were weaned in mid-September. By mid-October there were more weanlings on the beach than pups (Fig. 2).

Pup mortality from birth to weaning for 660 pups was 4.4% and the rate varied according to the breeding beach. Mortality for 237 pups born at La Armonia in large harems was 7.6% while it was 2.6% for 423 pups born in smaller harems at Punta Delgada (χ^2 = 9.0, df = 1, P < 0.05).

Weanling sex ratio (males : females) was not different from unity in 1984 (1.0:0.9, n = 687), 1988 (1.0:0.9, n = 202), and 1989 (1.0:1.1, n = 862) (G = 0.77, 0.32, 1.04, respectively, df = 1, P ≥ 0.38, 0.58, 0.31, respectively).

Departure of females after weaning pups—Females spent 28.2 ± 2.5 days (n = 38) ashore and departed 1.8 ± 1.2 d (n = 47) after they were seen copulating for the first time.

Pups remained within or close to the harem for 1.6 ± 1.2 days after weaning (n = 71, range = 0–5), but they were eventually chased away by lactating

females. Of 20 tagged pups followed daily after weaning, 19 were still at the same beach one month later, and at least 12 stayed ashore for about six weeks.

DISCUSSION

Our data on the timing of events of the breeding cycle at Península Valdés agree with partial information previously reported for the area (*e.g.,* Daciuk 1973, 1974; Le Boeuf and Petrinovich 1974; Scolaro 1976; Vergani 1985; Honigman 1988). Likewise, the variation in numbers during the breeding cycle and the relative timing of reproductive events at Península Valdés are similar to data from the largest populations of southern elephant seals, such as South Georgia (McCann 1980, 1985), Kerguelen (van Aarde 1980*a, b*), Macquarie (Hindell 1991) and Heard Islands (Burton 1986), and from the minor breeding sites such as Crozet (Barrat and Mougin 1978, Guinet *et al.,* in press), Gough (Bester 1980), Marion (Condy 1979) and King George Islands (Vergani and Stanganelli 1990). Typically, in all of these places southern elephant seals reproduce during the Austral spring, mortality from birth to weaning is low (2–5%) and pup sex ratio is unbiased. These parameters are similar for populations that are stable, decreasing or increasing in numbers.

Major differences in the breeding cycle between Península Valdés and other colonies are limited to harem size and to the date on which the peak number of adult females are hauled-out.

Harem size—Harems are smaller at Península Valdés than in other breeding colonies. At Kerguelen, females occur in harems with a mean of 76 and up to 739 individuals (Bester and Lenglart 1982). Average harems contain 40–50 females at Heard (Gibbney 1957), 100–300 at Macquarie and 70–75 at South Georgia Island (McCann 1980). Harems of up to 1,000 females were reported for Macquarie Island before the substantial decrease in size of that population (Carrick *et al.* 1962*a*). Harems are larger than at Valdés even for the smaller populations of Marion (Condy 1979) and Signy Islands (Laws 1956*a*).

Southern elephant seals breed in Patagonia under unusually low density conditions (Le Boeuf and Petrinovich 1974). Unlike other elephant seal rookeries (La Boeuf and Condit 1983, van Aarde 1980*b*) most females at Valdés are not densely packed, even during extreme high tides. Females are widely dispersed over 200 km of coastline, 80% of which is suitable habitat for reproduction (Lewis 1989, Campagna and Lewis 1992). The mean inter-harem distance at peak season reported for a 9-km coastline at Punta Norte was 400 m (Honigman 1988). The mode inter-harem distance for a longer stretch of beach (Punta Norte to Punta Cantor; Fig. 1), also at peak season, was 350 m (range = 50–600 m; Lewis 1989). Female dispersion decreases the potential for polygyny by increasing the energetic cost of monopolizing females (Emlen and Oring 1977), but low density aggregations confer, to a certain extent (see Campagna *et al.* 1992), some advantages to female pinnipeds due to decreasing the chances of mother-pup separation and pup mortality typical of large and dense seal harems with a high degree of disturbance (Le Boeuf and Briggs 1977, van Aarde 1980*b*). Female aggression, disruption of lactation, and mother-pup separation
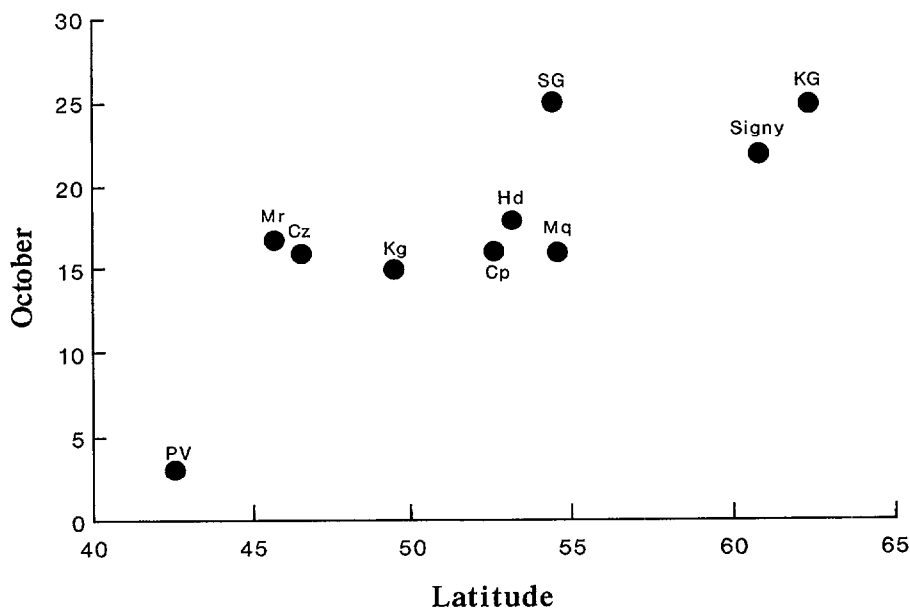
Figure 7. Time of the season when the maximum number of females are ashore as a function of latitude. [See references in McCann (1985) for colonies other than Península Valdés (this paper) and King George Island (Vergani and Stanganelli 1990).] PV: Península Valdés; Cz: Iles Crozet; Kg: Iles Kerguelen; Mr: Marion Island; Cp: Campbell Island; Hd: Heard Island; Mq: Macquarie Island; SG: South Georgia; KG: King George Island.

are unusual events at Península Valdés (Baldi and Campagna, unpublished observations). Pup separation from the mother is most often caused by males herding females and only rarely leads to pup mortality (Baldi and Campagna, unpublished observations).

The peak of the breeding season—The maximum number of females at Valdés occurred 2–3 wk earlier than in colonies located closer to the Antarctic Convergence (McCann 1980; Fig. 7). As factors influencing the timing and duration of pinniped breeding seasons are poorly known, we can only speculate about the proximate causes underlying clines in reproductive events between Patagonia and populations at higher latitudes. Despite risking being vague in our treatment of the issue, it may be useful, as a guidance to future work, to discuss some factors probably related to the timing of breeding in pinnipeds. Potential candidates are day length, thermal conditions and food availability. We will discuss these hypothetical proximate causes assuming that: (1) the length of gestation after implantation is constant (Boyd 1991), (2) the time during which the blastocyst remains dormant is variable (Daniel 1981) and (3) food resources off Península Valdés are abundant and available to the seals (Campagna and Lewis 1992, Anonymous FAO report 1991).

Photoperiod and reproduction—The timing of mating in some pinnipeds may be affected by environmental factors such as daylength (Daniel 1981, Temte

1985, Boyd 1991). Daylength may influence implantation of the blastocyst and synchronization of breeding (Boyd 1991). Therefore, physiological responses to the photoperiod may underlay differences in the timing of breeding events as a function of latitude. As southern elephant seals are found over a broad latitudinal range, populations would experience similar photoperiod conditions at different times of the year. If implantation occurs at the end of the molt (Laws 1956*b*), at the latitude of Península Valdés diapause would end when the days last about 14 h and are getting shorter. At this time of the year (end of January), the day length is different in other elephant seal colonies. Females at the latitude of Macquarie and South Georgia Islands would experience photoperiod conditions similar to the ones of Patagonia at the end of the molt, about three weeks later. This difference is similar to that found between those colonies regarding the peak of the breeding season.

However, the photoperiod-latitude hypothesis fails to explain the 10-day difference in breeding season peaks between South Georgia and Macquarie Islands, which are on the same latitude (McCann 1980; Fig. 7). Thus, variables beyond the length of the day should also be affecting the timing of breeding.

Climatic conditions—By breeding earlier in the spring than other populations, the seals of Patagonia would be less exposed to thermal stress by avoiding the warmer weather of late October and November. Elephant seals are susceptible to overheating (Whittow 1987) and show behavioral and physiological adaptations to avoid heat stress (White and Odell 1971, Honigman 1988). One-to-three week old pups may be the most susceptible to heat stress, judging from their quick and conspicuous response to high temperature and intense solar radiation (Campagna and Lewis, unpublished observations). Behavioral responses to hot weather may hamper male reproductive activity, cause mother-pup separation and result in female and pup harassment (Campagna and Vila, unpublished observations).

Food availability—Nutritional factors affecting the time of implantation of the blastocyst may also help to explain population differences in the timing of reproduction. Breeding, implantation and molting are apparently connected to body condition (Reiter *et al.* 1981; Boyd 1984, 1991). Therefore, the speed at which females partially recover their depleted energy reserves while foraging at sea after breeding may affect the timing of implantation.

Molting in elephant seals is an energetically expensive event during which animals shed large patches of epidermis and hair (Laws 1956*a*). It is then possible that the recovery of body mass and energy reserves after reproduction could affect the timing of the molt. If, due to abundance of food, the seals of Valdés recover their body reserves relatively quickly after breeding, then they would be ready to molt earlier than in other colonies. Females molt in Valdés 2–3 wk earlier than in other places (Laws 1956*a*, Carrick *et al.* 1962*b*, Bester 1988). Females marked during the breeding season were recorded back molting as early as five weeks after the end of lactation (Campagna, unpublished data). Most adult females at Península Valdés are advanced in the molt by the third week of January (Campagna and Lewis, unpublished data), suggesting that they have started the molt by late December. If the length of gestation is constant

and implantation is triggered by physiological cues associated to the cessation of molting (Bonner 1981, Boyd 1991), females would then implant and give birth earlier in Patagonia than at other colonies.

LITERATURE CITED

ANONYMOUS FAO REPORT. 1991. Exámen de la situación de los recursos pesqueros mundiales. Circular de Pesca 710 (7). Roma, FAO (Organización de las Naciones Unidas para la Agricultura y la Alimentación). 88 pp.

AARDE, R. J. VAN. 1980*a*. Fluctuations in the population of southern elephant seals *Mirounga leonina* at Kerguelen Island. South African Journal of Zoology 15:99–106.

AARDE, R. J. VAN. 1980*b*. Harem structure of the southern elephant seal *Mirounga leonina* at Kerguelen Island. Revue Écologie (Terre Vie) 34:31–44.

BARRAT A., AND J. L. MOUGIN. 1978. L'Elephant de mer *Mirounga leonina* de l'ile de la Possession, archipel Crozet (46°25'S, 51°45'E). Mammalia 42:143–174.

BELLISIO, N. B., R. B. LÓPEZ AND A. TORNO. 1979. Peces marinos patagónicos. Secretaría de Estado de Intereses Marítimos. Subsecretaría de Pesca. República Argentina. 279 pp.

BESTER, M. N. 1980. The southern elephant seal *Mirounga leonina* at Gough Island. South African Journal of Zoology 15:235–239.

BESTER, M. N. 1988. Marking and monitoring studies of the Kerguelen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in the Vestfold Hills. Hydrobiologia 165:269–277.

BESTER, M. N., AND P.-Y. LENGLART. 1982. An analysis of the southern elephant seal *Mirounga leonina* breeding population at Kerguelen. African Journal of Antarctic Research 12:11–16.

BONNER, W. N. 1981. Grey seal *Halichoerus grypus* Fabricius, 1791. Pages 111–144 *in* S. H. Ridgway and R. J. Harrison, eds. Handbook of marine mammals, Volume 2. Academic Press, London.

BOYD, I. L. 1984. The relationship between body condition and the timing of implantation in pregnant grey seals (*Halichoerus grypus*). Journal of Zoology (London) 203:113–123.

BOYD, I. L. 1991. Environmental and physiological factors controlling the reproductive cycles of pinnipeds. Canadian Journal of Zoology 69:1135–1148.

BURTON, H. 1986. A substantial decline in numbers of the southern elephant seal at Heard Island. Tasmanian Naturalist 86:4–8.

CAMPAGNA, C., AND M. LEWIS. 1992. Growth and distribution of a southern elephant seal colony. Marine Mammal Science 8:387–396.

CAMPAGNA, C., C. BISIOLI, F. QUINTANA, F. PEREZ AND A. VILA. 1992. Group breeding in sea lions: pups survive better in colonies. Animal Behaviour 43:541–548.

CARRARA, I. S. 1952. Lobos marinos, pinguinos y guaneras de las costas del litoral marítimo e islas adyacentes de la República Argentina. Fac. Cs. Vet. Univ. Nac. La Plata. 80 pp.

CARRICK, R., S. E. CSORDAS, S. E. INGHAM AND K. KEITH. 1962a. Studies on the southern elephant seal, *Mirounga leonina* (L). III. The annual cycle in relation to age and sex. CSIRO Wildlife Research 7:119–160.

CARRICK, R., S. E. CSORDAS AND S. E. INGHAM. 1962b. Studies on the southern elephant seal *Mirounga leonina*. IV. Breeding and development. CSIRO Wildlife Research 7:198–206.

CONDY, P. R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. South African Journal of Zoology 14:95–102.

DACIUK, J. 1973. Notas faunísticas y bioecológicas de la Península Valdés y Patagonia. X. Estudio cuantitativo y observaciones del comportamiento de la población del elefante marino del sur *Mirounga leonina* (Linne) en sus apostaderos de la Provincia de Chubut (República Argentina). Physis C 32:403–422.

DACIUK, J. 1974. Notas faunísticas y bioecológicas de la Península Valdés y Patagonia. XIII. Observaciones bioecológicas generales del elefante marino del sur *Mirounga leonina* en su apostadero de Punta Norte (Península Valdés, Pcia del Chubut, República Argentina). Physis C 33:203–214.

DANIEL, J. C. 1981. Delayed implantation in the northern fur seal (*Callorhinus ursinus*) and other pinnipeds. Journal of Reproduction and Fertility Supplement 29:35–50.

EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

GIBBNEY, L. F. 1957. The seasonal reproductive cycle of the female elephant seal, *Mirounga leonina* Linn., at Heard Island. A.N.A.R.E. Report (B) 1, 26 pp.

GUINET C. P., JAUVENTIN AND H. WEIMERSKIRCH. In press. Population changes, haul out pattern and movement of southern elephant seals on Crozet and Kerguelen Archipelagos. Polar Biology.

HINDELL, M. A. 1990. Population dynamics and diving behaviour of a declining population of southern elephant seals. Ph.D. dissertation, University of Queensland. 191 pp.

HINDELL, M. A. 1991. Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. Journal of Animal Ecology 60:119–134.

HINDELL, M. A., AND H. R. BURTON. 1988. The history of the elephant seal industry at Macquarie Island and an estimate of the pre-sealing numbers. Papers and Proceedings of the Royal Society of Tasmania 122:159–176.

HONIGMAN, L. 1988. Mating strategies in southern elephant seals, *Mirounga leonina*. M.S. thesis, University of California, Santa Cruz. 52 pp.

LAWS, R. M. 1956a. The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. Falkland Islands Dependencies Survey. Scientific Reports (London) 13:1–88.

LAWS, R. M. 1956b. The elephant seal (*Mirounga leonina* Linn.). III. The physiology of reproduction. Falkland Islands Dependencies Survey. Scientific Reports (London) 15:1–66.

LAWS, R. M. 1960. The southern elephant seal (*Mirounga leonina*) at South Georgia. Norsk Hvalfangst-Tidende 10 & 11:466–476, 520–542.

LE BOEUF, B. J., AND R. S. PETERSON. 1969. Social status and mating activity in elephant seals. Science 163:91–93.

LE BOEUF, B. J., AND L. F. PETRINOVICH. 1974. Elephant seals: interspecific comparisons of vocal and reproductive behavior. Mammalia 38:16–32.

LE BOEUF, B. J., AND K. T. BRIGGS. 1977. The cost of living in a seal harem. Mammalia 41:167–195.

LE BOEUF, B. J., AND R. S. CONDIT. 1983. The high cost of living on the beach. Pacific Discovery 36:12–14.

LEWIS, M. 1989. Dinámica de la población del elefante marino del sur, *Mirounga leonina*, en la Península Valdés. Ph.D. thesis, Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, Argentina. 107 pp.

LIOU, K.-N. 1980. An introduction to atmospheric radiation. Academic Press, New York.

MCCANN, T. S. 1980. Population structure and social organization of southern elephant seals, *Mirounga leonina* (L.). Biological Journal of the Linnean Society 14:133–150.

MCCANN, T. S. 1985. Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. Pages 1–17 *in* J. K. Ling and M. M. Bryden, eds. Studies of sea mammals in south latitudes. South Australian Museum, Adelaide, Australia.

REITER, J., K. J. PANKEN AND B. J. LE BOEUF. 1981. Female competition and reproductive success in northern elephant seals. Animal Behaviour 29:670–687.

SCOLARO, J. A. 1976. Censo de elefantes marinos (*Mirounga leonina*, L.) en territorio continental argentino. Informes Técnicos 1.4.2. Centro Nacional Patagónico. Puerto Madryn, Argentina.

TEMTE, J. L. 1985. Photoperiod and delayed implantation in the northern fur seal (*Callorhinus ursinus*). Journal of Reproduction and Fertility 73:127–131.

VERGANI, D. F. 1985. Estudio comparativo de las poblaciones de Antártica y Patagonia del elefante marino del sur *Mirounga leonina* (Linne, 1758) y su metodología. Publicación 15. Instituto Antártico Argentino. 94 pp.

VERGANI, D. F., AND Z. B. STANGANELLI. 1990. Fluctuations in breeding populations of elephant seals *Mirounga leonina* at Stranger Point, King George Island 1980–1988. Pages 241–245 *in* K. Hempel, ed. Antarctic ecology. Environmental changes and conservation. Springer-Verlag, Berlin.

VERGANI, D. F., M. N. LEWIS AND Z. B. STANGANELLI. 1987. Observation on haul-out patterns and trends of the breeding populations of southern elephant seals at Península Valdés (Patagonia) and Stranger Point (25 de Mayo-King George Is.). SC-CCAMLR-VI/BG 36:1–9.

WHITE, F., AND D. ODELL. 1971. Thermoregulatory behavior of the northern elephant seal, *Mirounga angustirostris*. Journal of Mammalogy 52:758–774.

WHITTOW, G. C. 1987. Thermoregulatory adaptations in marine mammals: interacting effects of exercise on body mass. A review. Marine Mammal Science 3:220–241.