Breeding season of the California sea lion (*Zalophus californianus*) in the Gulf of California, Mexico

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Abstract

Several years of census at two colonies in the Gulf of California (Los Cantiles, situated in the northern portion and Los Islotes in the south) were used to define the reproductive period of the California sea lion (*Zalophus californianus californianus*) in this area. The pattern of births (the length of the breeding period and the mean date of birth) is described using two models: a direct model, based on cumulative counts, and an indirect model, which related the photoperiod and the implanting of the blastocyte. The results of both models show that births begin earlier at Los Cantiles and that synchronization among females was less pronounced at Los Islotes. The mean arrival time of females was similar at both colonies, but differences were observed among the males. This suggests the existence of distinct competitive tactics that may be related to geographic position and the size of the colony. When results are compared with those from San Nicolas (California), it is clear that at Los Cantiles, the reproductive period is more prolonged, begins earlier, and that the time between giving birth and copulation for Gulf sea lions (intervals >30 days) is greater than that estimated for California (21 days).

Key words: breeding season, California sea lion, mating system, *Zalophus californianus*

Introduction

The mating system and the breeding season are important aspects for understanding the life history of a species (Gittleman, 1986) and for making comparisons between populations. The majority of pinnipeds show highly synchronized annual reproduction cycles (Boness, 1991), but when analyzed in detail, it is possible to detect interannual variations or differences between colonies of the same species. These variations may represent a response to environmental conditions, the genetic determi-

nation of the time of reproduction, or, to a lesser degree, the age of the females in the population (Duck, 1990; Boyd, 1991). The California sea lion (*Zalophus californianus californianus*), is a polygynous species (adult sex ratio of approximately 1:10 on mating grounds) (Jouventin & Cornet, 1980), which reproduces in southern California, along the west coast of Baja California, and within the Gulf of California (Le Boeuf *et al.*, 1983; King, 1983). The mating system is in the form of a moderate lek (Heath & Francis, 1983), with territories during the breeding season (Peterson & Bartholomew, 1967), and little synchronization of females in estrus, while the males remain sexually active throughout the breeding season (Emlen & Oring, 1977).

The size of the California sea lion population in California is estimated at about 112 000 animals (Lowry *et al.*, 1992) and the breeding season has been described by various authors (Peterson & Bartholomew, 1967; Odell, 1975; Heath, 1989; Francis & Heath, 1991). Odell (1975) presented the fullest description and reported that the length of the breeding season was about 10 weeks. The start of birthing was reported as the end of May, ending 1 month later (the end of June), with a maximum in the first days of June. Mating occurred between the first week of June and the last week of July. The interval between giving birth and copulation was estimated as between 15 and 21 days (Peterson & Bartholomew, 1967; Odell, 1975). The population residing in Mexico amounts to about 75 000 animals along the west coast of Baja and 30 000 in the Gulf of California (Le Boeuf *et al.*, 1983; Lowry *et al.*, 1992; Aurioles-Gamboa & Zavala-González, 1994). Information concerning the reproductive season for the species in Mexico is very poor. Brownell *et al.* (1974) mentioned that the period of birthing occurs in June along the west coast of Baja California; Aurioles-Gamboa & Le Boeuf (1991) reported a peak in births during the first week of June at a rookery in the southern Gulf of California, and Morales-Vela & Aguayo-Lobo
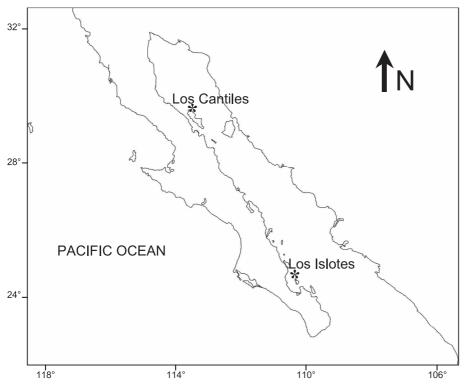
Figure 1. Location of Los Islotes and Los Cantiles California sea lion rookeries, Gulf of California, México.

(1992) presented data for a colony located in the northern Gulf of California. These authors mentioned that the breeding season begins in the second week of May with the arrival of the adult males and ends in the middle of August, when the last mating occurs; with the peak in births at the beginning of June.

Since no detailed characterization of the breeding season has yet to be made for the Gulf of California and because this population appears to display signs of genetic isolation (Maldonado *et al.*, 1995; Schramm, 2002), our objective was to describe the breeding season for the California sea lion of this region. Information from 17 years of census data at two rookeries (one in the northern and the other in the southern part of the Gulf) collected during the reproductive seasons between 1978 and 1998 is used to detect possible inter-annual or latitudinal differences.

Material and Methods

Census and reproductive event data (births and matings) were gathered from two sea lion colonies in the Gulf of California, Los Islotes and Los Cantiles (Fig. 1). Los Islotes (24°58′N and
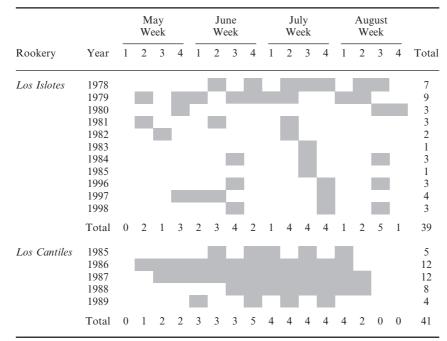
110°23′W) is located just to the north of the Espíritu Santo Island, in Bahía de La Paz, B.C.S. About 400 individuals (Hernández-Camacho & Aurioles-Gamboa, unpublished data) congregate there during the period of reproduction. Los Cantiles is situated at 29°53′N and 113°29′W, in the northeastern portion of Ángel de la Guarda Island, and close to 1300 sea lions (Aurioles-Gamboa & Zavala-González, 1994) reside there.

Data used

Data used in the analyses include 39 censuses from the periods 1978 to 1985 (Aurioles-Gamboa & Le Boeuf, 1983) and 1996–1998 (Hernández-Camacho & Aurioles-Gamboa, unpublished data) at Los Islotes, and 41 censuses from the period 1985–1989 at Los Cantiles (Morales-Vela, 1990), all between the months of May and August (Table 1). The record of matings was made during the 1987 season at two reproduction sites at Los Cantiles (Morales-Vela & Aguayo-Lobo, 1992), where up to 116 females congregate (García-Aguilar, personal communication). Insufficient information of matings was available for Los Islotes (we could record only five mating and three births).

Table 1. Censuses of California sea lion conducted during breeding seasons at Los Islotes and Los Cantiles, Gulf of California.

Rookery	Year	May Week 1	2	3	4	June Week 1	2	3	4	July Week 1	2	3	4	August Week 1	2	3	4	Total
Los Islotes	1978																	7
	1979																	9
	1980																	3
	1981																	3
	1982																	2
	1983																	1
	1984																	3
	1985																	1
	1996																	3
	1997																	4
	1998																	3
	Total	0	2	1	3	2	3	4	2	1	4	4	4	1	2	5	1	39
Los Cantiles	1985																	5
	1986																	12
	1987																	12
	1988																	8
	1989																	4
	Total	0	1	2	2	3	3	3	5	4	4	4	4	4	2	0	0	41

Data analysis

For both colonies, the interannual variation in the numbers of adult males, females and pups were analyzed using one-way ANOVA tests. The birthing season for each rookery was determined using the census data and cumulative frequencies. The mean date of birth was estimated in two ways. For the first, a logistical model (Trites, 1992) was applied using cumulative counts:

$$P_t = \frac{A}{1 + ce^{-kt}}$$

where, P_t is the number of pups, A, c and k are the parameters of the asymptote, the integration constant and the fixed rate of growth, respectively. Because the pup mortality in the first few months was less than 15% (Aurioles-Gamboa & Sinsel, 1988), when applying the model, the number of pups that die between counts was ignored and immigration and emigration were considered null. The average date of birth (B) was estimated according to Trites (1992) as:

$$B = \frac{-\ln\left(\frac{1}{c}\right)}{k}$$

with variance:

$$\mathrm{var}(B) = \left(\frac{1}{ck^2}\right)^2 \mathrm{var}(c) + 2\left(\frac{-\ln}{ck^3 \, \mathrm{var}(c) \, \mathrm{var}(k)}\right) + \left(\frac{-\ln c}{k^2}\right)^2 \mathrm{var}(k)$$

For the second approximation, we used the model proposed by Temte & Temte (1993), based on the analysis of captive animals and which relates the photoperiod (a function of latitude) and the dates of birth. In several studies by Temte, it has been demonstrated that, for most pinnipeds, implantation occurs close to the fall equinox, when 12 h of daylight are found around the world (Boyd *et al.*, 1999). The model assumes that implantation of the blastocyte, in response to the photoperiod, in California sea lions occurs 242 days prior to the date of birth. In applying the model, the date of the critical photoperiod of 11.48 h/day (the weighted regression mean estimated for the species) calculated for the latitude in question, and is used to define 'B' as:

B = date of photoperiod of 11.48 h + 242 days

Table 2. Mean (± standard deviation) of adult males, females and pups. Numbers in parenthesis represent the results of the inter-annual comparisons by rookery (all at *P*<0.05).

	Rookery/breeding seasons		
	Los Islotes 1978–1985	Los Islotes 1996–1998	Los Cantiles 1985–1989
Males	9.65 ± 3.52 (F=1.16, d.f.=7, 23)	24.90 ± 7.36 (F=4.28, d.f.=2, 7)	84.23 ± 20.47 (F=5.9*, d.f.=4, 34)
Females	67.90 ± 25.99 (F=1.91, d.f.=7, 23)	114.10 ± 21.08 (F=2.91, d.f.=2, 7)	571.84 ± 73.82 (F=2.13, d.f.=4, 34)
Pups	43.75 ± 9.22 (F=1.09, d.f.=7, 21)	107.67 ± 13.05 (F=0.87, d.f.=2, 7)	466.01 ± 27.47 (F=0.35, d.f.=4, 31)

LC=Los Cantiles, LI=Los Islotes.
*Significant difference in pup production at Los Islotes between periods t= − 9.28, d.f.=9, *P*=0.00001.

Table 3. Mean date of birth and duration of birth period for each rookery, estimated using the models proposed by Trites (1992) and Temte & Temte (1993).

	Mean date of birth			Duration of birth period	
Rookery	Cumulative counts (Trites, 1992)		Photoperiod (Temte & Temte, 1993)	Cumulative frequency	Photoperiod
Los Islotes	1978–1985 12 June ± 1.26 days	1996–1998 11 June ± 1.47 days	17 June	54 days	73 days
Los Cantiles	1985–1989 7 June ± 3.13 days	13 June	54 days	54 days	

This same model predicts the length of period of births as the number of days between the occurrence of photoperiods of 12.22 and 10.75 h/day at a given latitude, assuming that 95% of the blastocyte implantations are promoted by photoperiods in this range and that the length of time when births occur is always the same (Temte & Temte, 1993). Only the 1978–1985 period, with the data grouped in two-week intervals, was analyzed for Los Islotes, while data from 1985–1989, grouped on a weekly basis, were examined for Los Cantiles.
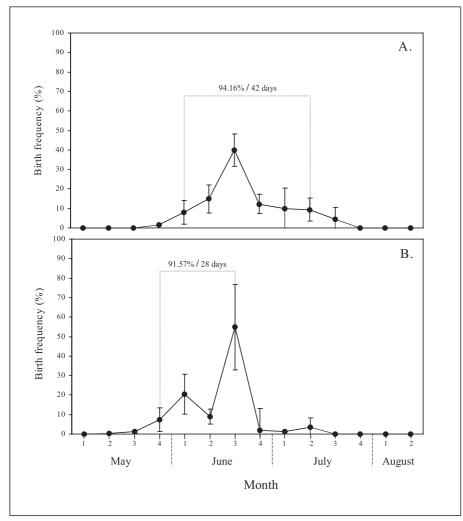
The variation in average number of female and male adults presents in the colonies during the breeding season was analyzed for each colony, and the sex ratio was estimated from the number of adult females divided by the number of adult males (the total number of males was used, ignoring whether they were territorial or marginal). The frequency of copulation was estimated only for Los Cantiles (using 1987's season data), throughout the season. The interval between giving birth and copulation was calculated as the difference (in days) between the mean date of birth and mating peak.

Results

Births
At Los Islotes, pup production for the 1996–1998 period was significantly greater than for the 1975–1985 period (Table 2). The mean date of births were estimated separately for 1978–85 and 1996–98 (Table 3). In both cases, birthing began in the fourth week of May and ended in the second week of July for 1978–1985, and the third week of July in 1996–1998. The period extended over 7 to 8 weeks, with a peak (40% of births) between 15 and 21 June (Fig. 2A).

No inter-annual differences in pup production were observed at Los Cantiles (Table 2). The period of births lasted 8 weeks, from the second week of May until the first week of July. Two maxima were observed: the first occurred from 1 and 7 June (21%) and the second, more intense (55%) during

Figure 2. Birth frequency of California sea lion in the Gulf of California, México. A. Los Islotes, and B. Los Cantiles.

the week of 15 and 21 June (Fig. 2B). Table 3 shows the average date of birth estimated by each method for both colonies.

Fluctuations of males and females number during breeding season
Los Islotes—The number of males in the colony did not vary significantly during the period of reproduction ($F_{15,15}=0.88$, $P>0.05$), although there was a small increase during the second half of May, which dropped again at the end of July and stayed constant until the end of August (Fig. 3A). In contrast, the number of females varied considerably ($F_{15,15}=3.60$, $P<0.05$): showing a significant increase starting in the second half of May and

reaching a maximum in the second week of August (Fig. 3A), with the increase being most marked from the beginning of June to early July.
Los Cantiles—The number of males varied significantly ($F_{12,27}=3.28$, $P<0.05$), with a notable increase in the first weeks of the season and reaching a maximum between the 8 and 14 July (Fig. 3B). The females displayed no variation ($F_{12,25}=1.45$, $P>0.05$), although a slight increase occurred from the first week of May until the second week of July.

The mean adult sex ratios at Los Islotes and Los Cantiles were 1:8.42 ± 3.53 and 1:7.80 ± 1.99, respectively, with no significant difference between colonies (t=0.41, d.f.=13, $P=0.69$). There were differences; however, between the two colonies
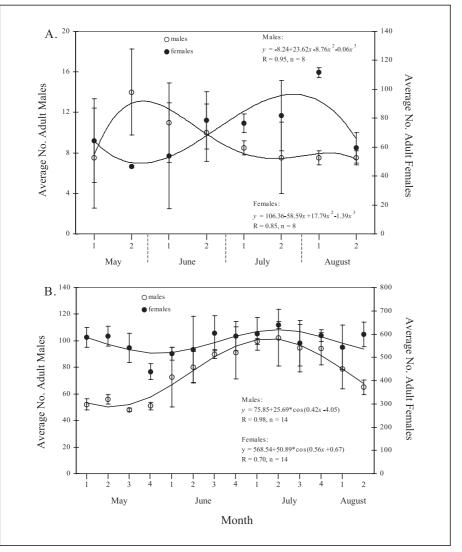
Figure 3. Changes in the average number of adults California sea lion males and females during the breeding season. A. Los Islotes 1978–85, and B. Los Cantiles 1985–89.

($\chi^2 = 31.11$, d.f. $= 14$, $P < 0.005$) in the sex ratio curves over the breeding season (Fig. 4). At Los Cantiles, a total of 86 copulations were recorded (74% of the females at the site), of which 98% were aquatic. The mating period began in the first week of June and ended in the second week of August. It lasted 10 weeks, with a peak between 1 and 15 July (44% of the copulations). At Los Islotes, the latest mating recorded was 20 August, and three females were observed both giving birth and copulating, the time between the events being 45, 62 and 63 days (García-A., unpublished data). If we considered the mean date of births and peak of mating at Los

Cantiles, the interval between births and matings was ≥ 30 days.

Discussion

Among many marine mammals, synchronization of births is associated with seasonality, food resources and predation pressure, for maximizing reproductive success (Peterson, 1968, cited in Trites, 1992). The two models used in these analyses present some differences in their results (6 days between models for both colonies), the photoperiod model providing a prediction while the other model provides a
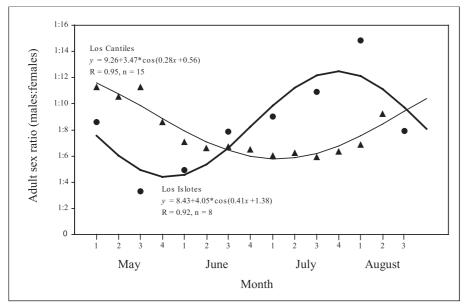
Figure 4. Changes in sex ratio among California sea lions at Los Islotes and Los Cantiles rookeries.

direct estimate. Nevertheless, both indicated that at Los Cantiles (northern Gulf), births precede those at Los Islotes (southern Gulf) by 4 to 5 days.

The length of the period of birthing estimated from the cumulative counts was similar for both colonies. The photoperiod model; however, gave contrasting results, the prediction for Los Islotes being almost 3 weeks longer than that for Los Cantiles. Furthermore, when the data for all years are combined for each colony, the distribution of births follows different patterns (see Fig. 2). At Los Cantiles two peaks in birth were observed, the second of greater intensity. This phenomenon has been noted previously by Odell (1975), and may reflect a strategy adopted by some females (possibly those of greater age and experience) for increasing the probability of survival of their pups in medium to large colonies. At Los Islotes, only one peak was observed. The lower intensity earlier peak was perhaps undetected due to the less observation effort than at Los Cantiles (see Table 1), or may simply not have occurred. Unfortunately, we have not enough data to test it.

Heath & Francis (1983) reported that, for *Zalophus c. californianus*, males and females arrive at the breeding grounds at the same time, but Morales-Vela & Aguayo-Lobo (1992) mentioned that the males arrive first, marking the beginning of the reproduction season. Our results reflect neither of these two patterns. The trend at both colonies was of a constant increase in numbers of females in the first part of the season, followed by a decrease in numbers until the end. Despite this similarity, there

were some important differences. The increase in numbers began a week earlier at Los Cantiles and at Los Islotes the period of increasing females covered 8 weeks, compared to six at Los Cantiles. At both colonies, the most rapid increase coincided with the greatest frequency of births: from early June to early July (5 weeks) at Los Islotes, during which 84% of births occurred, while at Los Cantiles it was between early and mid-June (3 weeks), also the period accounting for 84% of births. These females apparently arrive to give birth and nurse. The continuous increase until August at Los Islotes, and to mid-July at Los Cantiles reflects the arrival of non-pregnant females, who arrive and mate after most of the earlier arrivers have given birth, as has been documented for this and other otarid species (Trillmich, 1990; Boness, 1991). These results, together with the length of the period and the dates of births and arrival time of the females, suggests that there is less synchronization among females at Los Islotes.

The fluctuation of the males number was different at each colony. One showed an increase in numbers over almost the entire length of the season, while at the other, an initial exit of males was followed by a period of relatively constant numbers. The differences may be due to geographic position and, possibly, on the degree of aggressiveness of the males. Los Cantiles is located in the Midriff Islands ('Grandes Islas') region, which harbours approximately 64% of the sea lion population of the Gulf of California (Aurioles-Gamboa & Zavala-González, 1994). The continuous increase

Table 4. Comparison of the breeding season of *Zalophus californianus* at San Nicolas Island, California, and Los Cantiles, Gulf of California.

	San Nicolas[a]	Los Cantiles
Location	33°15′N	24°53′N
	119°30′W	110°23′W
Duration of the breeding season	9.5 weeks	13 weeks
Births		
Start	≈20 May	≈8 May
Duration	5 weeks[1]	8 weeks[1]
	6.5 weeks[2]	8 weeks[2]
Mean date	≈4 June[1]	7 June[1]
	10 June[2]	13 June[2]
Copulations		
Start	≈5 June	≈4 June
Duration	7 weeks	10 weeks
Peak	≈30 June	1–15 June
%Aquatic	60	98
Interval between birth and copulation	≈21 days	≥30 days

[a] Source: Odell, 1975.
[1] Estimated for cumulative counts.
[2] Estimated for photoperiod model.

in males may be due to marginal animals from neighbouring island colonies that come to Los Cantiles to reproduce. Los Islotes, on the other hand, is the most southerly of the reproductive colonies and is relatively isolated (Aurioles-Gamboa & Zavala-González, 1994; Schramm, 2002), so that immigration of males from other colonies does not occur, or is much reduced. In moderate colonies over an extensive area with greater resources (such as Los Cantiles), it is very probable that male aggressiveness is less than in a small colony in a compact area (Sutherland, 1996). Therefore, it is possible that some males at Los Islotes are very aggressive animals that move others off the breeding areas, forcing them to abandon the colony even before most of the females arrive to reproduce.

The mating system of the California sea lion is that of a modified lek (Heath & Francis, 1983), which occurs when defence of the females or important resources are too costly for the males, because of the mobility of the females over a relatively large area (Emlen & Oring, 1977; Davies, 1991). Due to the characteristics of the lek, it has been demonstrated that, although it is true that the dominant males generally achieve greater reproductive success, it often happens that peripheral males succeed in occupying territories when dominant ones move out (Höglund & Robertson, 1992). Because of this, the sex ratios were estimated considering all of the males, regardless of whether they

were marginal or dominant. The sex ratio is a measure of the degree of polygyny and is strongly influenced by the habitat (Bartholomew, 1970; Clutton-Brock, 1989). The instantaneous mean adult sex ratios (about 1:8) were similar for both colonies, falling within the estimated range for this and other otarid species (Jouventin & Cornet, 1980). Because of the behaviour of the males; however, the individual sex ratio curves were different over the season. During the period that should have represented the greatest frequency of copulation, at Los Cantiles the sex ratio was below standard (1:6), while at Los Islotes it stayed within the typical range (1:11), which suggests different competitive strategies. Male strategy depends on the number of females, their spatial distribution and the synchronization of estrus (see original sources in Radespiel *et al.*, 2002). As discussed previously, the two colonies present differences in each of the three factors, so it is not surprising that the strategies may be distinct. At Los Islotes, the number of females is reduced, they are found in a small area and estrus is poorly synchronized, so that conflicts among males must be common and dominance must play an important role in access to females.

Finally, the mating period (only for Los Cantiles) begins approximately 3 weeks after the first pups are born and ends 4 weeks after the final births. It has been estimated that female California sea lions are receptive 21 days after giving birth (Odell, 1975) and that the period of estrus is between 5 and 8 days

for most otarids (Boyd *et al.*, 1999). Even considering the possibility that a female copulates several times and that the records obtained correspond to only one such event, our observations suggest that, in the Gulf of California, the interval between giving birth and mating is greater than 30 days.

In summary, what appears clear is that the reproduction period begins first at Los Cantiles, that the period of giving birth at Los Islotes is more prolonged (or at least of equal length) even though the size of the colony is much smaller, which suggests less synchronization among the females at Los Islotes. Furthermore, the behaviour of the males was different at each colony, suggesting the existence of distinct mating tactics. Since both colonies are within the Gulf of California it was assumed that there were no differences in the patterns of reproduction, but it is clear that a latitude component exists that influences the timing and mating behaviour of the California sea lion.

Even greater differences are encountered when comparing what is observed in the Gulf and in colonies further north, on the coast of the Pacific Ocean. The characteristics of the reproduction period at Los Cantiles are compared with those reported by Odell (1975) for the colony of San Nicolas, 106 km southwest of Los Angeles, California (Table 4). It is obvious, among other things, that synchronization of reproduction is less at Los Cantiles. The observable differences in characteristics and in the length of the period of reproduction may be due to latitudinal position and different environmental conditions (Temte & Temte, 1993; Boyd, 1996). Clearer differences are seen when making the comparisons with the subspecies *Z. c. wollebaeki*, which lives on the Galapagos Islands (at 2°S), whose tropical climate induces little seasonal variation. For this subspecies, Trillmich (1986) reported a reproductive period of 5 months.

Acknowledgments

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