Effects of the Lunar Cycle on the Galápagos Fur Seal, *Arctocephalus galapagoensis*

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Summary. During the 1977 and 1979 reproductive periods of the Galápagos fur seals a census taken in the mornings and evenings at Cabo Hammond, Fernandina, showed a marked, synodic lunar rhythm in numbers of animals ashore. About twice as many fur seals were ashore at full moon than at new moon. By use of two independent Fourier analysis methods, the curve of the morning counts is shown to lag 15°–20° of the lunar month behind the curve of the evening counts. The lunar effect is demonstrated for males, females, and immatures. The rhythm is also seen is demonstrated for males, females, and immatures. The rhythm is also seen in attendance data from 13 individually marked females, all but one nursing young. Reproductive events show the lunar rhythm much less markedly than do numbers ashore. This and the clear rhythm in immature numbers make it very likely that the rhythm is a year-round phenomenon, independent of reproduction.

There is no reason to assume that fur seals stay on land during moonlit nights especially for social interaction. It is then hypothesized that fur seals avoid moonlight at sea. If so, the peak of numbers ashore at full moon and the negative phase angle difference of the evening curve against the morning curve can be explained with the shift, and the varying duration and brightness, of the moonlit part of the night over the lunar cycle. Two hypotheses which might account for this moonlight avoidance are discussed: (1) predator (shark) avoidance and (2) varying feeding efficiency of the fur seals due to the influence of moonlight on the vertical distribution of prey.

Introduction

Via tidal rhythms and direct light effects, the lunar cycle profoundly influences the ecology and reproductive cycles of many marine invertebrates (Alldredge and King in press; Enright 1975; Hauenschild 1960; Palmer 1974; Neumann and Heimbach 1979). Lunar effects have also been described for some fish (review in Gibson 1978) and terrestrial vertebrates (e.g., Fitzgerald and Bider 1974; Gwinner 1967; Morrison 1978; Pearson 1960a and b).

No lunar influence on marine mammals has as yet been conclusively shown, which is especially surprising with regard to the coast-living pinnipeds. There is a faint suggestion of such an influence, shown by the patterning of dentin deposition in the teeth of *Otaria byronia* (Laws 1962), and perhaps an influence, deduced from whaling data, on the grouping tendency in sperm whales (Holm and Johnsgård 1959). At their hauling-out sites and breeding grounds pinnipeds are constantly exposed to the tides, and their prey may also be influenced in following the vertical migration of plankton, for example, by the rhythm of lunar light intensity.

During a study of the reproductive behavior of the Galápagos fur seal (*Arctocephalus galapagoensis*, Heller 1904) a strong periodicity in numbers of fur seals ashore was found to be synchronized with the synodic lunar month. This paper describes this effect and may help in formulating hypotheses about the behavior and ecology of pinnipeds in their marine environment, in which direct studies are extremely difficult. The results are also of practical consequence for the evaluation of census data.

Materials and Methods

Study area

The study was done at Cabo Hammond (91° 37′ W, 0° 28′ S), Fernandina, the southwest corner of the westernmost island of the Galápagos archipelago. Fernandina Island is the most active volcano of the Galápagos islands (Hall 1977) and is totally uninhabited and free of introduced higher plants and animals. The whole coastline of the study area consists of lava, some parts being recent lava flows and others large boulders smoothed by wave action.

Counts

Fur seal counts were made during the reproductive season which lasts from about August to November (Trillmich 1979). The number of pups steadily increases during this time, accounting for about one-third of the animals ashore at the end of the season. To adjust for this trend, the total number of animals ashore is always given without pups. Fur seals were assigned to one of the following age/sex categories: (1) territorial male; (2) nonterritorial male; (3) adult female; (4) immature (of unknown sex up to about three years of age); (5) pup (young of the year, not yet moulted) (6) adult (of unknown sex). Most animals could easily be assigned to one of the first five categories. Animals in category 6 averaged only 1%–2% of the totals.

All counts were made by one person (F.T.) to eliminate possible variance through different walking speeds, search efforts, or experience. Little tunnels and caves abound along the coastline, but most animals stayed in the open early in the morning and late in the evening when the counts were made. The animals were counted in the course of a slow walk along a 670 m (1977) or 530 m (1979) section of coastline at Cabo Hammond and the total width of the coastline used by the fur seals (up to about 20 m) was censused. Animals can usually be approached to within a few meters without being obviously disturbed. A count lasted 1–1.5 hours, depending on the number of animals ashore. In 1977 counts were made every 5 days between August 20 and November 13 (Fig. 1). In 1979 only one lunar cycle (August 22 to September 21) was covered and counts were unevenly spaced, taking place

daily only around full moon (Fig. 2). In both years morning and evening counts were made. Morning counts began as soon as there was light enough to identify the animals (about 5:30 A.M.). Evening counts began between 4:30 P.M. and 5:00 P.M., ending at or shortly after sunset.

Female Attendance Data

In 1979 the presence or absence of 12 females with pups or one- or two-year-old immatures and one adult female without young were noted 1–5 times daily. From these data the duration of their stays ashore was calculated, on the assumption that a female seen at or after 6:00 P.M. and at or before 6:00 A.M. of the following day had been ashore all night. If her presence at either of these times could not be confirmed, a question mark was put down for that night. If she was observed at neither of these times it was assumed that she had spent the night at sea.

Distribution of Births

In 1979 pups were counted at least every 4 days, but generally daily, and all newborn pups were marked by clipping a bit of fur on their backs. From these data a very accurate curve of the distribution of births over the reproductive season was obtained.

Fourier Analysis of the Lunar Cycle

Data on lunar phases were taken from nautical tables (Instituto Oceanographico, Guayaquil, Ecuador). To analyze the periodicity in the census data the interval between two new moon phases was set at 360° and the times of the counts were converted to degrees accordingly. To obtain an objective description of the features of the morning and evening counts, a Fourier analysis was performed first with an ansatz symmetric about some central phase φ_0:

$$y = \sum_{n=0}^{N} a_n \cdot \cos(n \cdot (\varphi - \varphi_0)). \tag{1}$$

The central phase φ_0 and the coefficients a_n were iteratively optimized using a least-squares criterion (Marquardt 1963). For a detailed state-of-the-art discussion see Chambers (1973).

The order of harmonic approximation was restricted to 3 ($N=3$) which proved sufficient for the data distribution. The rounded coefficients obtained are summarized in Table 1. The dimension of the phase is degrees, that of the coefficients number of animals. One can tell from Table 1 that a_3 is comparable to its error, which supports our argument of $N=3$ being sufficient. The central phase and the coefficients are well defined. The resynthesis of the approximants is shown in Fig. 3a and b.

One might argue now that the symmetric ansatz (1) leads to artificial extra phase-shifts, since the 1979 data seem to be asymmetric around the central phase (Fig. 2). We therefore secondly represented the data by an unrestricted Fourieransatz:

$$y = \sum_{n=0}^{N} a_n \cdot \cos n \cdot \varphi + \sum_{n=1}^{N} b_n \cdot \sin n \cdot \varphi. \tag{2}$$

Least squares estimates of the parameters a_i and b_i may be obtained using standard linear analysis algorithms. We chose $N=3$ and resynthesized the approximants (Fig. 4a, b).

Table 1. Parameters of the Fourier analysis method (1) and estimated standard deviations calculated according to the method of Marquardt (1963). Initial values chosen were $\varphi_0 = 160°$, $a_0 = 200$, $a_1 = 80$, $a_2 = a_3 = 40$. Parameters were optimized by iteration, leading to convergence in ten steps

Censuses	φ_0	a_0	a_1	a_2	a_3
1977 Morning	174 ± 6	273 ± 12	83 ± 17	49 ± 18	46 ± 34
1977 Evening	151 ± 9	225 ± 12	59 ± 18	46 ± 17	6 ± 14
1979 Morning	195 ± 5	274 ± 12	88 ± 17	64 ± 16	54 ± 17
1979 Evening	180 ± 6	256 ± 12	59 ± 19	60 ± 17	33 ± 19

Now we may determine the phase-angle difference ($\Delta\varphi$) between the curves of the morning and evening counts by cross-correlation. Let $f_1(\varphi)$ approximate the morning census and $f_2(\varphi)$ the evening census. Define: The mean:

$$\bar{f}_i = \int_0^{2\pi} f_i(\varphi) \, d\varphi.$$

The product moments:

$$s_{ij}(\Delta\varphi) = \int_0^{2\pi} (f_i(\varphi + \Delta\varphi) - \bar{f}_i)(f_j(\varphi) - \bar{f}_j) \, d\varphi.$$

The cross-correlation (C):

$$C(\Delta\varphi) = \frac{s_{12}(\Delta\varphi)}{\sqrt{s_{11}(0)s_{22}(0)}}.$$

The cross-correlation as a function of phase-angle difference $\Delta\varphi$ is drawn above in Fig. 4a and b. Its maximum yields the most likely phaseangle difference between the two functions.

Results

In 1977 and 1979 the numbers of fur seals ashore in the Cabo Hammond study area showed marked peaks around full moon and clear minima near new moon (Figs. 1, 2), with about twice as many animals ashore at full moon. Morning and evening censuses both show the lunar rhythm with the evening census almost always producing lower totals than the morning census (Figs. 1 and 2). This is explained through the transition of numbers ashore from morning to evening. Regular counts during daytime show a slight increase in numbers ashore until about 8:00 or 9:00 A.M., depending on the weather; thereafter, numbers drop slightly toward noon as some animals hide in caves or spend the hours around noon resting in the water in front of the colony. In the late afternoon (4:00 to 5:00 P.M.) another weak maximum is reached, followed by a rapid drop in numbers in the evening when many individuals leave the rookery to forage at sea.

At the time of increasing half moon, numbers ashore augment more rapidly in the evenings than in the mornings, sometimes even becoming larger in the evenings. With decreasing full moon numbers fall far more rapidly in the evenings than in the mornings. This leads one to suspect a phase angle difference between the curves of morning and evening counts. We estimated the value of the phase angle difference using Fourier analysis methods (1) and (2). A comparison of the data and their Fourier synthesis according to method (1) is given in Fig. 3a and b for 1977 and 1979, respectively. The error of the representation may thus be judged by close visual inspection. For the phase angle difference ($\Delta\varphi$) between morning and evening censuses, we obtained with this method:

$$\Delta\varphi = \varphi_{0,\text{ morning}} - \varphi_{0,\text{ evening}} = 23° \pm 11° \quad (1977)$$
$$\Delta\varphi = \varphi_{0,\text{ morning}} - \varphi_{0,\text{ evening}} = 15° \pm 7° \quad (1979)$$

Thus there is a clear phase angle difference between morning and evening censuses that, taking into account the error bounds – estimated from the standard deviations of the parameters given in Table 1 – is indistinguishable between 1977 and 1979. The Fourier synthesis using ansatz (2) is shown in Fig. 4a and b for the 1977 and 1979 data, respectively. Comparison of Figs. 3 and 4 shows that there is no marked difference between the representation of the data by (1) and (2). With method (2) the maximum
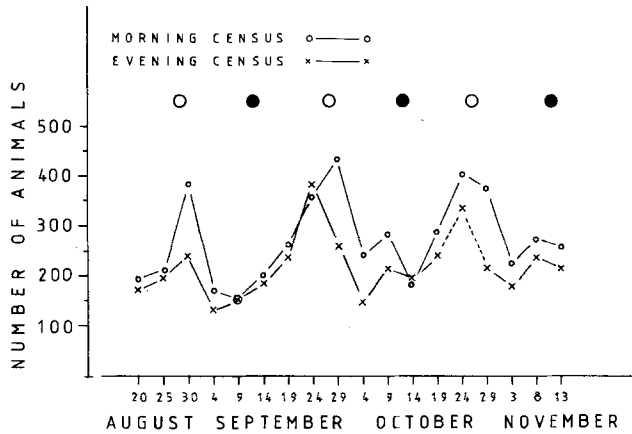
Fig. 1. Morning and evening census data from 1977 (670 m coastline). Total of animals ashore excluding pups. o full moon, ● new moon. On October 24 the evening census was not completed because of darkness. The total was estimated (*broken line*) as the sum of counted animals plus the average percentage (16%) of fur seals found on the missing piece of coastline in the preceding and following four evening censuses
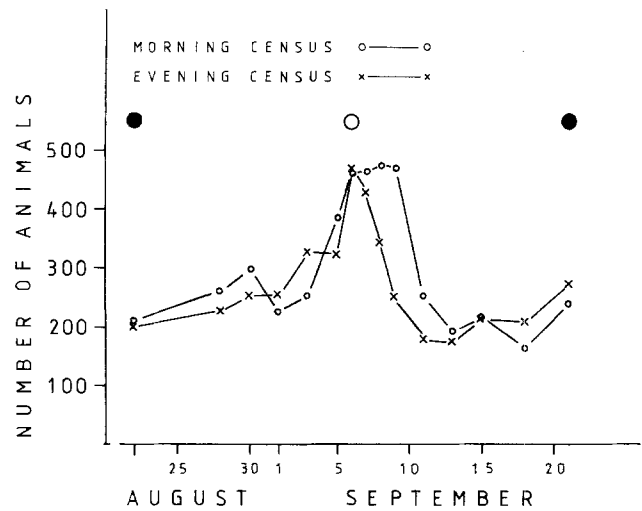

Fig. 2. Morning and evening census data from 1979 (530 m coastline). Total of animals ashore excluding pups. Note the rapid drop in the numbers of fur seals ashore in the evenings after full moon in comparison with the plateau in the morning census. Symbols as in Fig. 1

of the cross-correlation function yields the most likely phase angle difference between the morning and evening counts. One obtains:

$$\Delta\varphi = 17° \quad (1977)$$
$$\Delta\varphi = 15° \quad (1979).$$

The previously calculated phase angle differences are confirmed and the agreement between the phase shifts in the 1977 and 1979 data is even better. Taking the results of the two methods together, one obtains a phase angle difference between morning and evening censuses in both 1977 and 1979 of between 15° and 20° of the synodic lunar month, or 30 to 40 hours (see Figs. 3 and 4).

The doubling of numbers ashore around full moon and the negative phase angle difference of the evening curve against the morning curve are our main arguments for interpreting the lunar rhythm in numbers ashore as a moonlight-avoidance response (see Discussion).

Numbers of males, females, and immatures ashore follow the same rhythm, proving that all animals are influenced in a similar manner by the underlying factor(s) (Fig. 5a, b). Males, although lowest in numbers, show the lunar cycle quite markedly. It is at present unclear if the total male population is smaller than the female population, i.e., if the tertiary sex-ratio is strongly
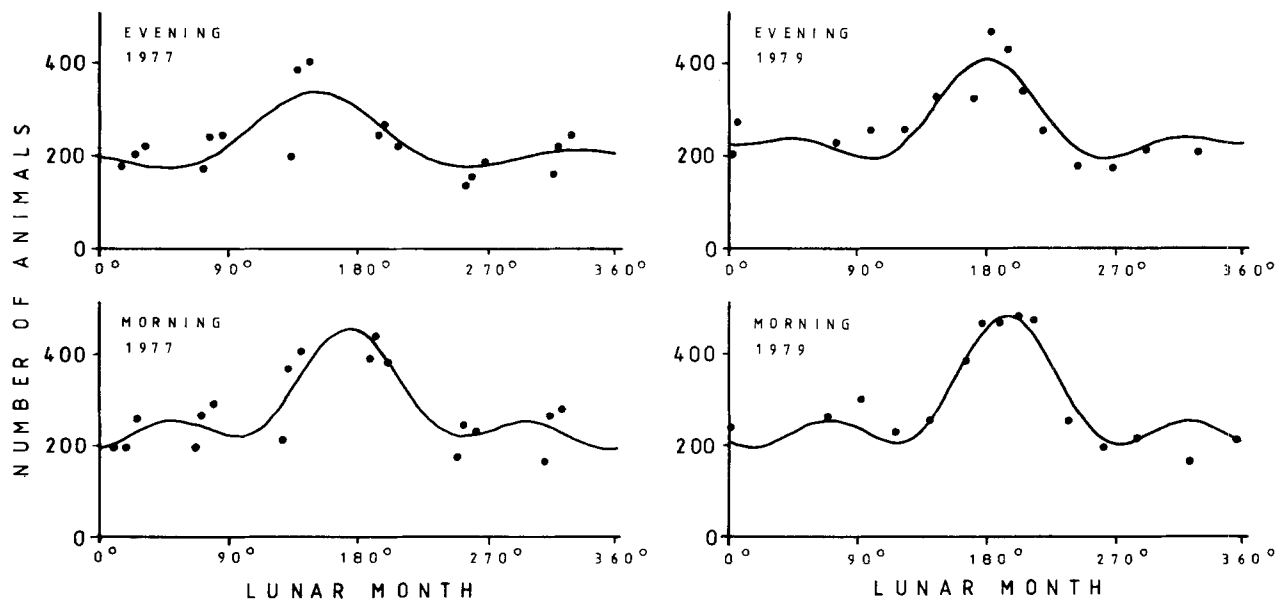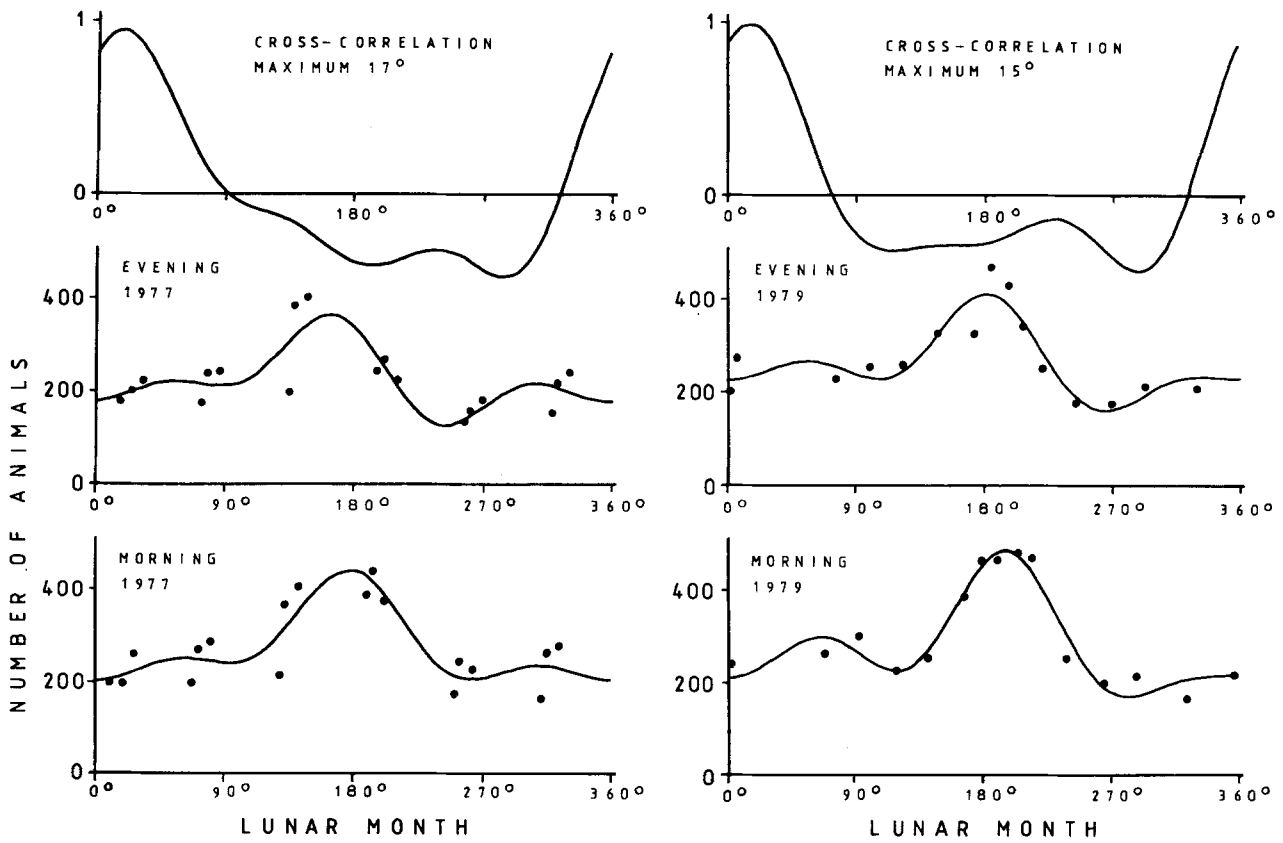

Fig. 3a, b. Representation of the lunar cycle of numbers of fur seals ashore by the resynthesized curves of the symmetric ansatz of the Fourier analysis (1). **a** Data points and resynthesized curves from the 1977 censuses. *Above*: Evening data. *Below*: Morning data. **b** The same for the 1979 data

Fig. 4a, b. Representation of the lunar cycle of numbers of fur seals ashore by the resynthesized curves of the unrestricted ansatz of the Fourier analysis (2) **a** Data points and resynthesized curves from the 1977 censuses. *Above:* Cross-correlation function for evening and morning curves. *Middle:* Evening data. *Below:* Morning data. **b** The same for the 1979 data
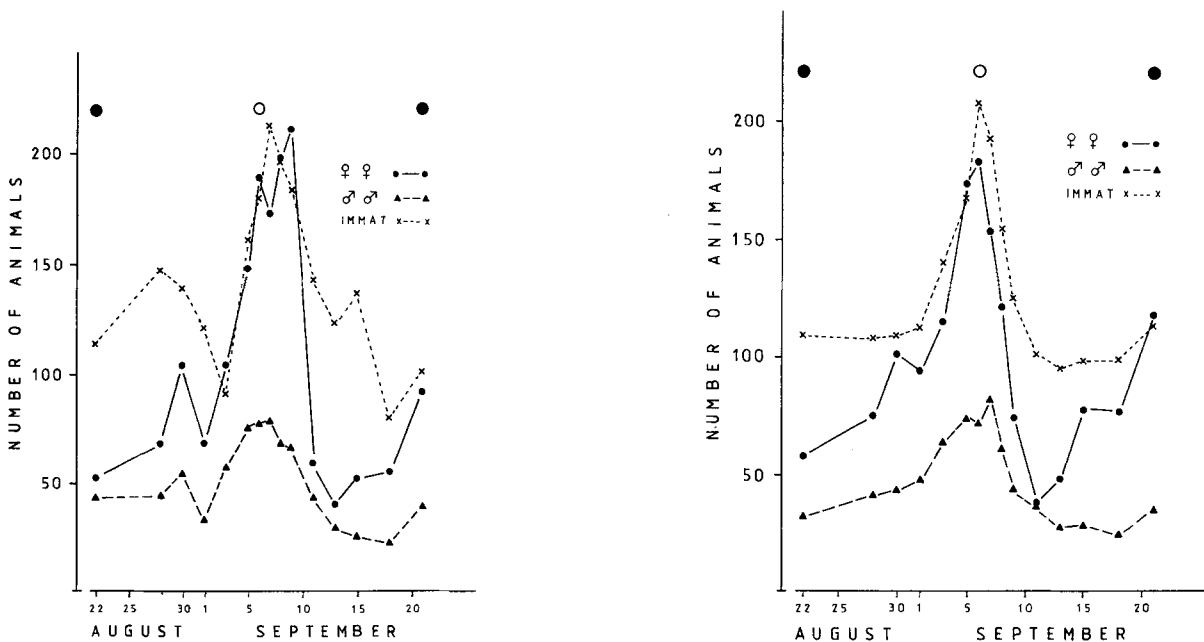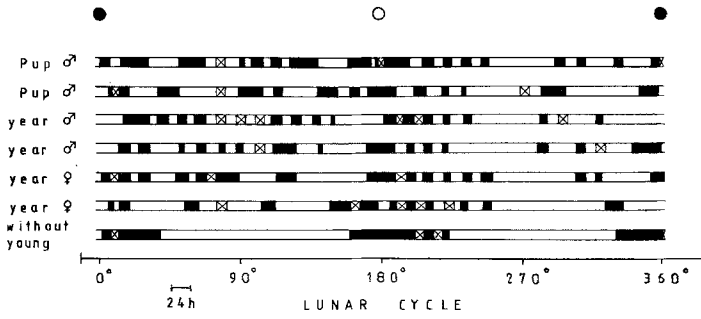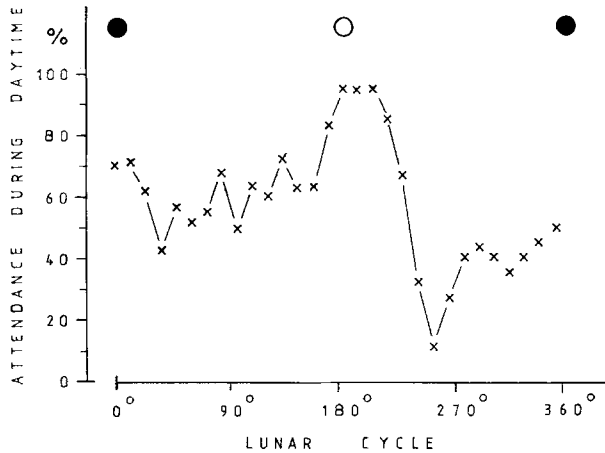

Fig. 5a, b. Number of males, females, and immatures counted ashore in 1979. All three classes of fur seals show almost the same periodic pattern. **a** Data from morning censuses (*left*) **b** Data from evening censuses (*right*)
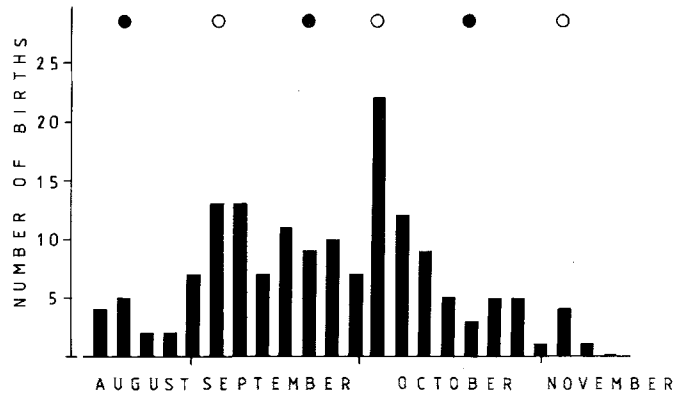
Fig. 6. Presence (black) of 7 individually marked fur seal females on land. Continuous observations over each lunar cycle in 1979. Crosses indicate insufficient observations for one day or one night. The key on the left indicates age and sex of the female's young (if she had one)

Fig. 8. Number of newborn pups for the 1979 reproductive period added up for consecutive 4-day intervals. First interval is August 15–18, last November 7–10. (No pups were born on November 11 and 12)

Fig. 7. Attendance of females with young during daytime over the lunar cycle. Each point gives the percentage of females present during the day at the given phase angle of the lunar cycle. Observations were made over about 20 lunar cycles (of 13 females). Thus each point is calculated from, on average, 20 ± 1.2 observations

The female curve exhibits the greatest amplitude. This appears logical, since no females are excluded from the colony (as the nonterritorial males are) and all of them have to forage at sea for themselves and many for their pups or immatures as well. Females with young return every few days to the colony to nurse their young. Consequently, at any given time, a large proportion of the total female population is found ashore.

It is assumed that animals not seen ashore in the study area do not go ashore elsewhere. This is almost certainly valid for females nursing a pup or an immature. Also the few marked males, some subadults, and a few ousted territorial males were regularly observed to return to the same sites within the study area, which suggests that they behave similarly. Given this assumption, theoretically the greatly varying numbers ashore can come about through one of the following types of behavior:(1) fur seals may stay at sea for longer intervals around new moon than around full moon; (2) they may go out for equal periods but more frequently around new moon than full moon; (3) a combination of (1) and (2) might be responsible for the observed rhythmical changes in numbers ashore.

The observed attendance of 12 females who nursed a pup or immature agrees best with possibility (3) (Fig. 6). Most females were almost continuously present around full moon and tended to be absent longest around waning half moon. This latter observation corresponds with the minimal numbers of animals ashore at waning half moore in the population censuses (Fig. 5a, b). Presumably the fur seals are especially hungry after their long stay on land around full moon and tend to make up for their weight loss through longer foraging sojourns immediately afterward. Compared with the mothers, one marked female without young remained at sea for unusually long periods (Fig. 6, lowest line). It is at present unknown if this is typical for females without young.

The summation of about 20 such lunar cycles observed in 13 different females produces a lunar rhythm of numbers ashore roughly similar to the population censuses (compare Figs. 1, 2, 7). Of the females with young, 95% were seen ashore on days around full moon (Fig. 7). Presumably the same is true for the full moon nights, but data are insufficient to verify this at present.

The curve of pup births in 1979 has one single pronounced peak in early October (Fig. 8). This curve, spanning three months, may perhaps be modulated with the frequency of the lunar cycle,

skewed, or if males tend to forage at sea for longer intervals, thus reducing the proportion of males on land. These data were obtained during the reproductive period when almost the whole coastline is claimed by territorial bulls, and nonterritorial males cannot move freely in the colony. They tend to hide in lava tunnels and crevices, still further reducing the number of males available to be counted. Repeated observations of a few tagged males in the main study area show that the lunar rhythm does not influence the detectability of males, i.e., that the rhythm of male numbers ashore is not caused by differing hiding behavior.

The immature category is composed of three age classes; one-, two-, and a few three-year-olds. One-year-old immatures of the Galápagos fur seal get a large fraction of their alimentation from mothers' milk (unpublished data), rarely foraging for themselves at sea; at all times a large majority of them are found ashore. The two- and three-year-olds, normally foraging for themselves, leave the colony much more frequently, and it is predominantly these that produce the lunar periodicity in immature numbers ashore.

causing weak local minima at new moon and maxima near full moon. Pup births mark periods of sexual activity, since females copulate on average 7–10 days postpartum. But the influence of the lunar cycle is shown much less clearly in reproductive activity than in the number of animals ashore. That immatures show the lunar cycle so markedly highlights its independence of reproductive events. Although our measurements took place during breeding time, we believe periodicity in animal numbers ashore is unrelated to reproduction and a consequence of the synodic lunar cycle. Therefore, it is expected to be a year-round phenomenon.

Discussion

The census work on the Galápagos fur seal at Cabo Hammond, Fernandina, revealed a lunar influence on the numbers of animals ashore. This effect has the following attributes: (1) it can be demonstrated for all sex and age classes investigated; (2) it shows a phase angle difference between morning and evening census of 15°–20°; (3) it is assumed to be a year-round phenomenon.

One plausible hypothesis for this lunar rhythm would appear to be that the animals are better able to interact on land in the moonlight than during dark nights. If so, during full moon nights one would expect more interactions per animal than during new moon nights. As even in daylight intensive interactions between fur seals are almost always accompanied by loud vocalizations, increased activity should be reflected in more calls per animal. This does not happen. Call counts (10 min for every hour of the night, see Fig. 9) on one new moon and one full moon night showed roughly a doubling of the total number of calls heard in all 10-min intervals taken together during the full moon night (571 versus 329 calls in the new moon night), which is what one would expect if about twice as many animals were on shore on full moon nights. Furthermore, the activity pattern is the same on both nights, with minimum activity around midnight when the full moon is brightest, and this further weakens the idea of any special social activity during the full moon night. Fights between males and copulation were observed on both moonless and moonlit nights. Moreover, the animals reacted to a moving human even on new moon nights, which indicated that they were able to see movement under starlight conditions. Thus the hypothesis that fur seals stay on land during moonlit nights especially for social interactions is rather unlikely.

We must then turn to the fur seal's life at sea for an explanation of the lunar influence on numbers ashore. The census curves (Figs. 1, 2) could be explained most easily if we assume that fur seals avoid moonlight at sea. Galápagos fur seals normally stay on land in the daytime and leave the colony at dusk to feed at sea during the night (Trillmich 1979), although the animals show clear signs of thermal stress during the day. The shift of the moonlit part of the night over the lunar cycle could explain the pattern and the phase angle difference of the morning and evening curves (Figs. 1 and 2). With a waxing moon the first half of the night is moonlit. If the animals were trying to avoid moonlight at sea, they should stay on land longer in the evening, which would then, given the same foraging time, delay their return to the colony next morning. Consequently, evening counts would tend to be higher than the corresponding morning counts. This should become more and more pronounced as the moon becomes brighter and full moon approaches. Around full moon only very few animals forage at all (Fig. 7). After full moon the first half of the night becomes dark, whereas the second part is brightly
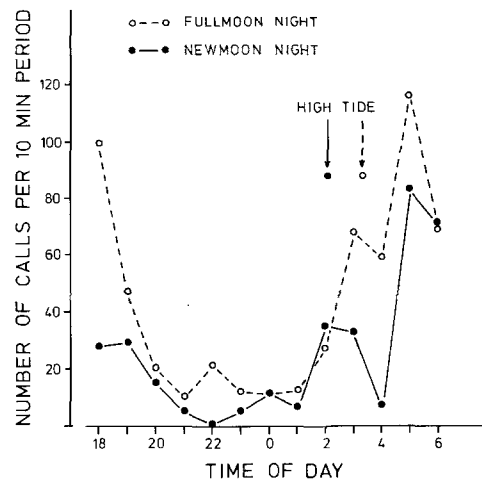

Fig. 9. Calling activity in the fur seal colony during one full moon and one new moon night. The incoming tide (*arrows*) *leads to* a peak of calling activity in both nights

lit. According to the hypothesis of moonlight avoidance at sea, animals should leave the colony in the afternoon and return during the night, certainly before the morning census. This would account for the observed rapid decrease in numbers ashore in the evenings after full moon, and the plateau in the morning numbers (Fig. 2). So far, these events have been discussed as if the animals went out for one night only. As we know from the female attendance data, this is certainly not the case; but longer sojourns at sea would produce the same rhythm of numbers ashore, if the probability of their initiation and completion followed the rules outlined above. Thus moonlight avoidance at sea appears to be a plausible proximate cause for the observed changes in numbers.

What ultimate causation might underlie this behavior? Two factors, discussed here singly but more likely to occur in combination, may account for the observed behavior of the fur seals:

1) Predator avoidance

Sharks, which abound in Galápagos waters, attack fur seals. Quite regularly adults and immatures were seen with healed shark bite marks in their fur or on their flippers, and recently wounded animals were also observed occasionally. From telemetry observations on free-living Blue sharks (*Prionace glauca*) it is evident that they hunt mainly at night (Siarotta 1974; cited in Nelson 1974). Myrberg (1969) also noted that the activity of Sharpnose sharks (*Rhizoprionodon* sp.) increased when turbidity increased or ambient light levels decreased. A fur seal surfacing and diving during his nightly feeding at sea, and perhaps every now and then splashing about on the surface and thrashing a wounded fish or squid, is open to auditory and perhaps also olfactory detection by sharks. Splashing noises have been shown by Myrberg (1970, 1971) to be highly effective in attracting sharks from considerable distances. From observations and experiments on the feeding behavior of sharks (Hobson 1963; Gilbert 1963) we know that sharks direct the final attack on a prey object visually. If a fur seal is brightly silhouetted against the moonlit surface of the sea, he will be very vulnerable to attacks from below, especially as he cannot see down into the depths from which the shark attack might come. Fur seals can afford to stay at sea during the day because under daylight conditions it is much easier to

see a shark approaching from below. Thus predation pressure through sharks could explain the avoidance of moonlight by fur seals as a strategy to decrease the risk of fatal attack.

One might object that on moonlit nights fur seals should be able to feed more efficiently because they should find it easier to spot their prey against the moonlit surface, just as the sharks presumably do. Their avoidance of the sea during moonlit nights would then be a cost/benefit compromise between preying and being preyed upon: the chance of the fur seal to catch prey probably decreases with decreasing light (but see below), but so does the chance of being fed upon by sharks. If the fur seal can get enough calories during moonless nights, then there would be no good reason to go out during dangerous moonlit nights as well. In other words, the enemy dominates the behavior: as ambient light levels increase, the cost of staying at sea increases much faster than the benefit.

Moonlight avoidance has also been found in terrestrial animals, which reduce their activities during the moonlit parts of the night (Anderson 1966; Doucet and Bider 1969; Erkert 1974, 1977; Fitzgerald and Bider 1974; Jahoda 1973; Lockard and Owings 1974; Morrison 1978; O'Farrell 1974; Pearson 1960b; Stutz 1973; Turner 1975; Usman et al. 1980). Some of these authors have also interpreted this moonlight avoidance as predator (e.g., owl) avoidance. The problem with the predator-avoidance hypothesis is that it is very difficult to prove without measurement of mortality under moonlight and moonless conditions.

2) Varying Feeding Efficiency due to Moonlight Influences on the Vertical Distribution of Prey

Galápagos fur seals feed on squid (Clarke and Trillmich 1980) and small fish (*Sardinops* sp., Scombridae; unpublished data). It has been shown that light influences the behavior and vertical migration of squid (Young and Mencher 1980; Boden and Kampa 1967) and that the vertical migration of some demersal plankton species is influenced by lunar light (Alldredge and King in press). In both cases the animals tend to rise toward the surface with a drop in light intensity, and to move downward with increasing light intensity. If this were true for the food species of the fur seals, they would have to dive deeper on moonlit than on new moon nights to obtain their prey (assuming that their prey species follow the vertical migration pattern of larger zooplankters). Their prey may actually stay too deep during the day as well as on moonlit nights to be within diving reach. Kooyman et al. (1976) measured a maximum diving depth for the Northern fur seal (*Callorhinus ursinus*) of 190 m, but 91% of all dives (2,957) were to depths shallower than 51 m. But squid may be far deeper than this (Boden and Kampa 1967). Consequently, the fur seal's feeding efficiency might be much higher on dark nights.

No data on the vertical migration of the food species concerned are available, so we cannot even be sure that some food organisms do not actually migrate toward the surface on moonlit nights, as suggested by the success of light fishing (Blaxter and Currie 1967). To test this hypothesis it is planned to measure the rates of weight gain of animals feeding at different times of the lunar month to estimate their feeding efficiency.

Implications for the Evaluation of Census Data

It is obvious that such a marked and predictable fluctuation in numbers ashore must be taken into account for the evaluation of population census. The best census time is the early morning. Population counts not made at full moon will have to be corrected by an appropriate factor to allow an estimate of population size at full moon. As a first approximation, one may assume that near full moon 95%–100% of the animals are ashore (compare Fig 7). This would provide a minimum estimate of population size.

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