

TIME BUDGET IN GALAPAGOS FUR SEAL PUPS: THE INFLUENCE OF THE MOTHER'S PRESENCE AND ABSENCE ON PUP ACTIVITY AND PLAY

by

WALTER ARNOLD and FRITZ TRILLMICH¹⁾

(Max-Planck-Institut für Verhaltensphysiologie, Abteilung Wickler, D-8131 Seewiesen, W.-Germany)

(With 12 Figures)
(Acc. 20-IX-1984)

Introduction

The young of many mammalian species initially depend entirely on mother's milk to obtain the energy necessary for maintenance, activity and growth. This strong link between mother and young leads one to expect that the mother's activity pattern and the rate of energy transfer directly influences the activities of her young. Fur seals are suitable species in which to examine such influences, as females regularly leave their pups in order to forage at sea for several days. They spend about one day ashore suckling the single young between foraging trips (BONNER, 1981; GENTRY, 1981; TRILLMICH, in press). In this way pups are periodically exposed to food deprivation and at other times have high rates of energy intake. They are also among the most precocial mammalian young and show almost all adult behavior patterns very early in their ontogeny, in play at least.

The cyclical availability of food would lead one to assume that hunger also varies cyclically. Hunger is usually considered to be a dominant motivational system and play to be a weak, subordinate behavior tendency (EIBL-EIBESFELD, 1980) so one would predict that play activity varies with the cycle of maternal attendance. Studies on other species showed a reduction in play activity upon long term reduction in food availability (BALDWIN & BALDWIN, 1972; DASMAN & TABER, 1956; GEIST, 1971; LOY, 1970; RICHARD & HEIMBUCH, 1975; RUTISHAUER & WHITEHEAD, 1972; SCHALLER, 1972, 1977; ZIMMERMANN *et al.*, 1975). Even during short

¹⁾ We would like to thank J. LAMPRECHT, U. REYER, M. TABORSKY, P. VOGEL and W. WICKLER for critical comments on various drafts of the manuscript. B KNAUER expertly prepared the figures and Lesley GARDINER kindly corrected the English. This is contribution no. 379 of the Charles Darwin foundation.

term food deprivation without any chronic effects play activity was found to decrease rapidly in some studies (BALDWIN & BALDWIN, 1976; MÜLLER-SCHWARZE *et al.*, 1982; ROSENBLUM *et al.*, 1969; SOUTHWICK, 1967). However, the play activity of young otariids is very conspicuous, even in the sometimes prolonged absence of their mothers (GENTRY, 1974).

We investigated how pups of the Galapagos fur seal (*Arctocephalus galapagoensis*) regulate their level of activity and play when cut off from their source of food, the mother. The activity budget recorded for answering this question is the first available for the young of any otariid seal. It also allows us to look for sex differences in play behavior of the pups of this species.

Material and methods

Individually marked fur seal females and their pups were studied in a colony at Cabo Hammond, Fernandina, Galapagos during the reproductive season of Aug. to Oct. 1980.

Time budgets were obtained from observations every minute on the minute (ALTMANN, 1974). Using this method, the percentage frequency of a behavior gives a close estimate of time actually spent performing it. This method is prone to error with very short or infrequently occurring behavior patterns so we simultaneously recorded the frequency of occurrence of short behaviors. No important differences between the two sampling methods were found, except in playfighting (Fig. 9). All results are therefore presented as percentage of time spent in a behavior.

Weights of pups in the mothers' absence were determined to the nearest 5 g for 9 male and 6 female young. Pups were usually captured for weighing around 0600 and 1800 hrs, and placed in a small aluminium box on top of a balance; afterwards they were returned to the site of capture.

Definitions of terms:

lying (ly) = inactive, in prone position;

sitting (si) = inactive, sitting;

walking (wk) = any site change or consistent attempt to do so by very small pups;

suckling (su) = actively sucking on searching for teats;

looking (lk) = attentively looking at an object or in one direction after stopping or turning the head; often pups look backwards by raising the head without turning it;

sniffing (sn) = sniffing at any object except conspecifics;

sniffing at fur seal (sF) = sniffing any body region of another fur seal, with vibrissae turned forward. This includes naso-nasal greeting (MILLER, 1975);

grooming (gr) = scratching with the claws of a hind flipper, rubbing the fur or face with a front flipper and rubbing the pelage with the side or the top of the head;

wiggling (wg) = pup wiggling its flippers but not moving from the spot;

exhaling into the water (ew) = pup pushing its head underwater into a little puddle or pool and exhaling through the nose;

chewing (cw) = pup chewing on its own flippers or on inanimate objects;

play-fighting (pf) = pups trying to hold each other with their teeth and shaking their opponent when they have a firm grip; with their necks against each other trying to push

their partner backwards and, at the same time, attempting to bite his flanks or front flippers. This rarely involves more than two pups.

Biting the mother was also recorded as pf if the pup was not searching for teats at the time. This behavior occurred only in very young pups;

head jearking (hj) = quick raising of the head with a sideways shaking motion, often accompanied by a simultaneous jumping forward. This behavior appears to be a play invitation as it very frequently preceded pf. It also occurs in object play, e.g. with rocks;

chasing (ch) = chasing other pups, crabs or marine iguanas. A very young pup may also chase after its mother's flippers when she flips them about to chase off flies. Pups sometimes try to catch their own hind flippers while waving them; both behaviors were included in this category;

fighting (fi) = vocalizing with open mouth while pressing the vibrissae closely against the head (threat; MILLER, 1975). The pup may actually bite an unyielding opponent;

appeasing (ap) = pup giving a high pitched call, rapidly shaking its head laterally, with small amplitude and simultaneously fencing the mouth of the opponent with wide mouth. Vibrissae are turned forward (submission, MILLER, 1975);

calling (ca) = calls of fur seal pups and mothers are described in TRILLMICH (1981). Calling is rare and occurs almost exclusively in interactions with the mother;

hidden (hi) = when an animal was invisible from the observer's position on the minute;

opportunity for contact (oc) - while noting every behavior pattern we also observed whether a pup was close enough to sniff at another fur seal, except its own mother, without having to walk. This allows us to estimate how the frequency of interaction is determined by the availability of potential interaction partners;

activity bout - these begin with the first different behavior pattern after ≥ 5 min of lying if activity lasts for ≥ 5 min. The end is similarly defined as the onset of ≥ 5 min of lying. Daytime activity bouts are those beginning or ending between 0600-1800 hrs;

time active = sum of all day or night activity bouts.

To allow a more concise presentation of results behavior patterns were sometimes grouped into more comprehensive categories (e.g. Fig. 9); repetitive and seemingly functionless behaviors were assumed to be play (FAGEN, 1981):

- 1) *exploratory behavior* (Eb) = lk and sn;
- 2) *play* (Pl) = pf, ch, hj, cw, ew and wg;
- 3) *interactions* (It) = sF and ca;
- 4) *others* (O) = fi, ap and hi.

Background information on presence and absence of mother Galapagos fur seals

After parturition mothers remain on land with the pup for about one week (TRILLMICH, in press). Thereafter mothers alternate between periods of absence, when foraging at sea, and periods of attendance. The duration of these periods varies individually and systematically with the phase of the lunar month (TRILLMICH & MOHREN, 1981). Median attendance duration is 22.5 hrs (range 1.5-75 hrs) and median absence 33.5 hrs (range 3.5-127.0 hrs) (TRILLMICH, in press). Mothers observed in this study were absent for a max. of 4 days.

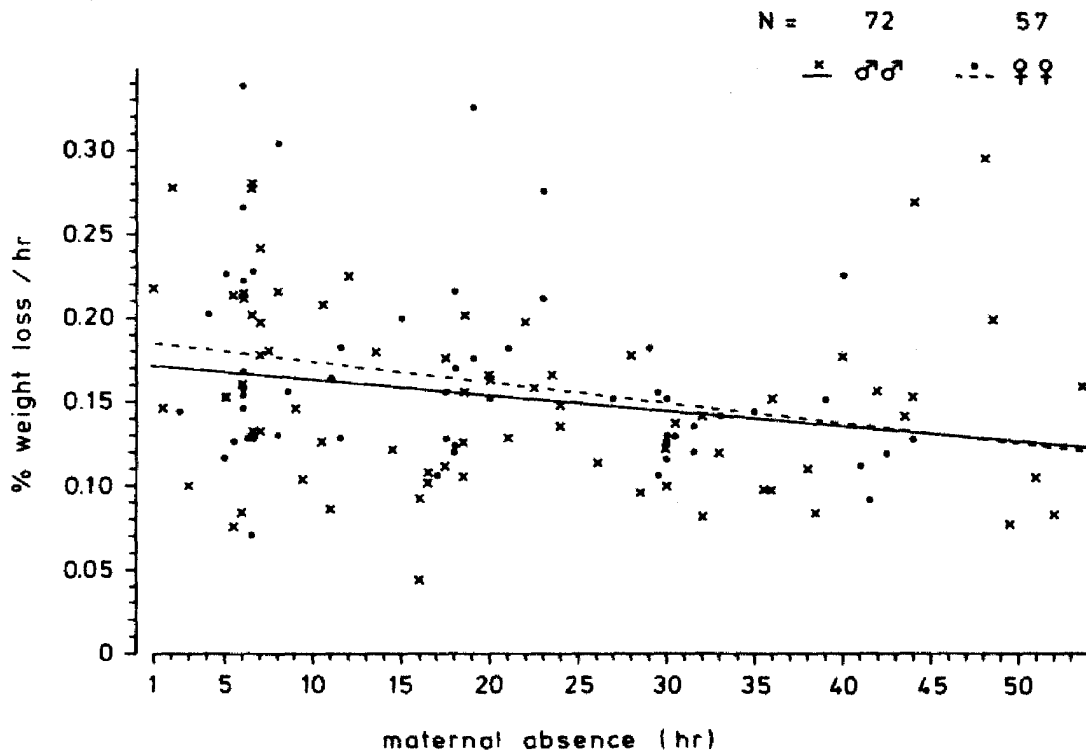


Fig. 1. Rate of weight loss per hour (as percentage of body weight) over the period of maternal absence. Rate of weight loss was plotted for the median hour between two weighings. Regression for male pups: $y = 0.172 - 0.001x$; $r = -0.226$; $0.1 > p > 0.05$. Regression for females: $y = 0.187 - 0.001x$; $r = -0.265$; $p < 0.05$.

Results

Weight loss of pups during the mothers' absence.

A pup can hardly ever steal milk from a female which is not its mother as fur seal females are very aggressive towards strange pups (TRILLMICH, 1981). Consequently, pups continuously lost weight until the return of their mothers (Fig. 1). Percentage weight loss per hour decreased the longer the pups were left alone, for the time period measured ($y = 0.178 - 0.001x$; analysis of covariance: $df = 126$, $p = 0.006$). This decrease in the rate of weight loss was not significantly different between the sexes (neither in slope nor in intercept). No differences in rates of weight loss were found between day and night nor morning and afternoon.

Average percentage weight loss per hour was 0.16 ± 0.06 . When multiplied by the median absence duration of mothers (33.5 hrs) this gives an average weight loss of pups, between visits, of $5.3 \pm 1.9\%$. For

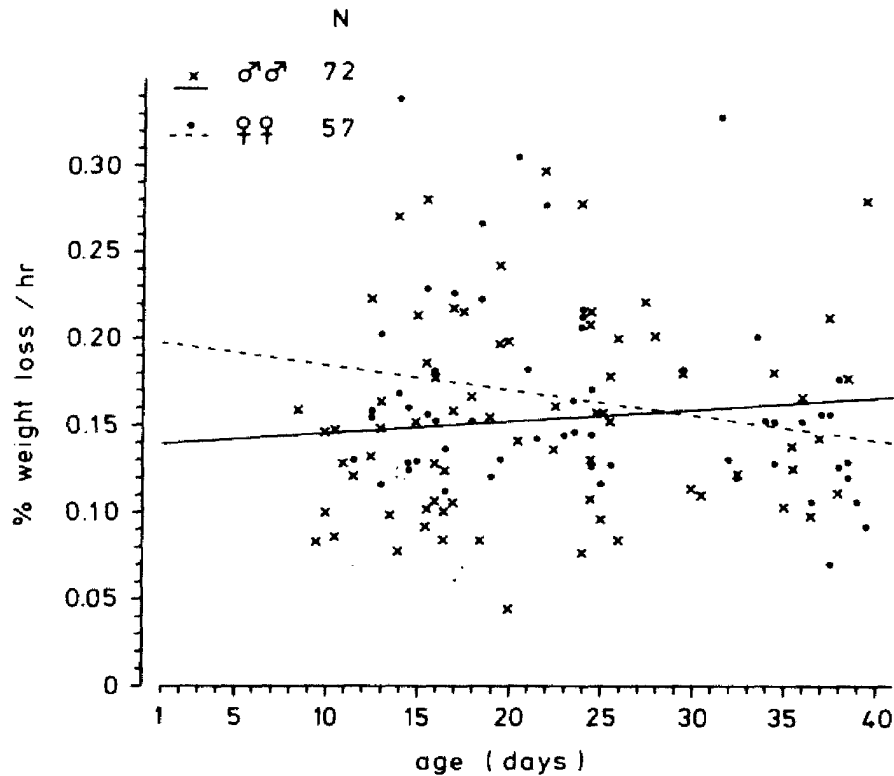


Fig. 2. Rate of weight loss of pups per hour (as percentage of body weight) in the mothers' absence as a function of age. Regression for males: $y = 0.138 + 0.001x$; $r = 0.110$; n.s. Regression for females: $y = 0.201 - 0.002x$; $r = -0.250$; n.s. The slopes of regression are significantly different (see text).

the longest absence of a mother, 127 hrs, weight loss of the pup would amount to approximately 20%. Thus we conclude that pups experienced increasing hunger (and thirst?) when their mothers were foraging.

Rate of weight loss depended on the age of pups (Fig. 2). Data were obtained for male and female pups at very similar ages and are therefore directly comparable (males: 21.7 ± 8.5 days; females: 24.0 ± 8.9 days). However, rate of weight loss in female pups appeared to decrease with age but showed the opposite trend in males. The slopes of regression for rate of weight loss with age were significantly different between male and female pups ($df = 125$, $p = 0.046$; analysis of covariance).

The mother in attendance: influence of age on time active and day/night differences in pup behavior

Material

The behavior of two male pups during their mothers' attendance on land was observed continuously during all daylight hours (0600-1800) at different ages (1, 3, 5, 9/12, 21/22,

29/29/31, 59/60 days after birth; total observation time: 195 hrs). They were also observed for a total of 52 night hrs at the ages of 1, 3, 28/29, 30, 59 and 61 days.

Results

Time active.

As pups grew older they became active for an increasing percentage of the daytime observations. The same trend could not be ascertained for the night observations, although regression slopes did not differ significantly. The intercept of the percentage of observation time active against age was, however, significantly lower for night than for day (Fig. 3). The slope of time active against age was not significant for the daytime observations of pups aged 12-31 days. Although this could be due to our small sample size, the influence of age on time active appears to be negligible over this age interval.

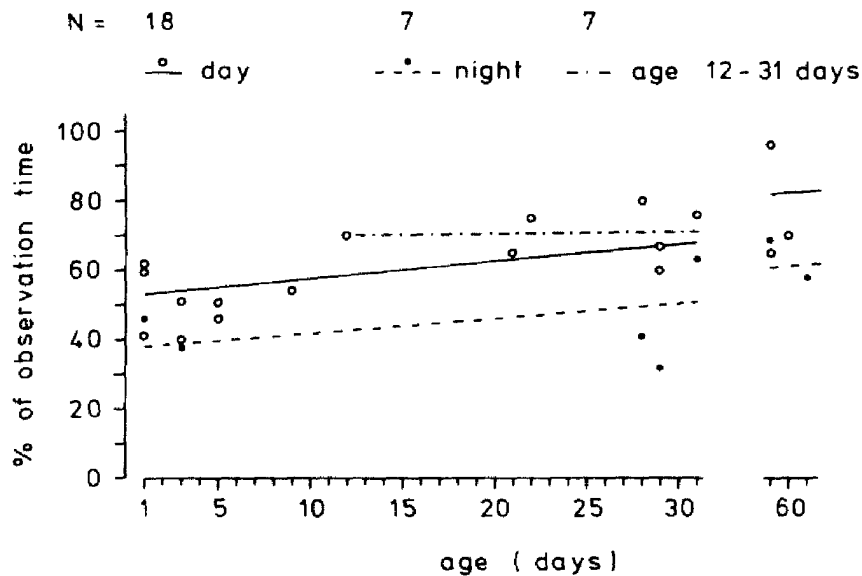


Fig. 3. Increase in proportion of time active with age. Regression for daytime: $y = 52.45 + 0.486x$; $r = 0.698$; $p < 0.01$. Regression for night: $y = 38.05 + 0.381x$; $r = 0.647$; n.s. the intercepts of the two regression lines are different at $p < 0.001$. Regression for daytime between the ages 12 and 31 days: $y = 68.65 + 0.074x$; $r = 0.070$; n.s.

Since *time active* occupied a more or less constant proportion of the *observation time* over this age range, we shall refer to the proportion of time spent in each behavior pattern during time active rather than during the total observation time. This eliminates the variance associated with the

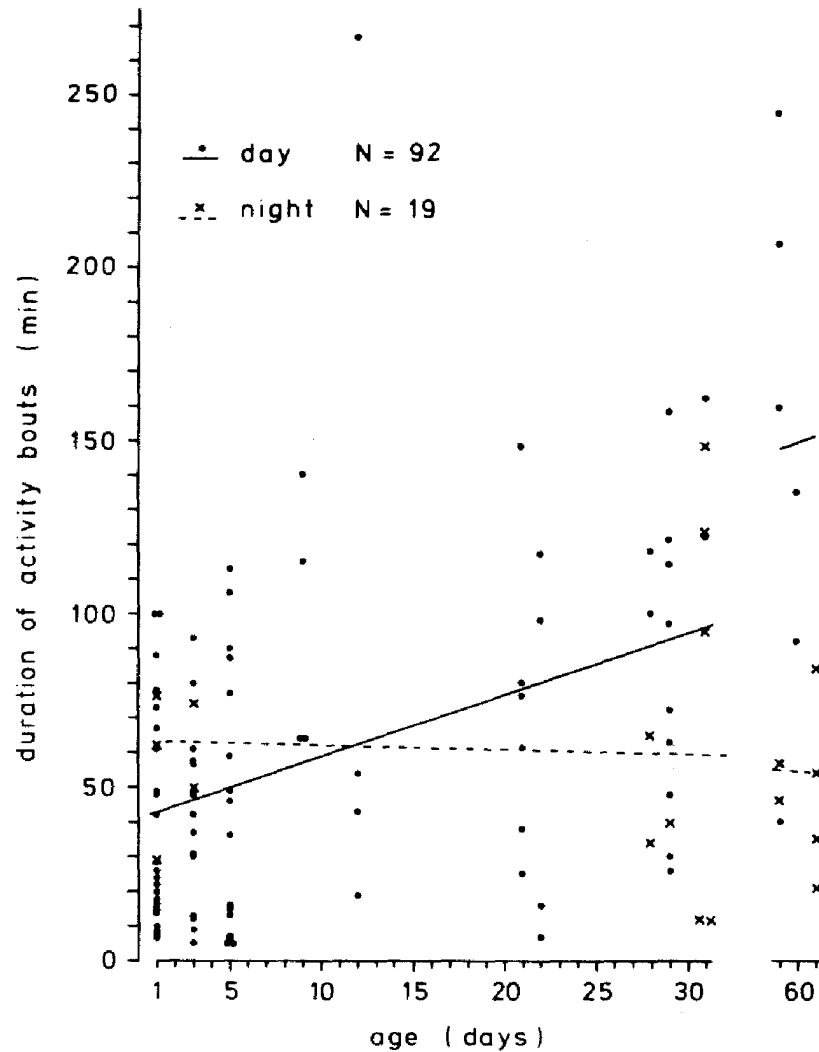


Fig. 4. Dependence of the duration of pup activity bouts on age. Regression for daytime: $y = 40.14 + 1.811x$; $r = 0.544$; $p < 0.001$. Regression for night: $y = 63.78 - 0.154x$; $r = 0.098$; n.s.

difference in the absolute time spent active by pups on different days. Only Figs 3, 5 and 12 refer to observation time.

Duration of activity bouts.

Activity bouts lengthened with increasing age during the day but not at night (Fig. 4). The number of activity bouts per hr decreased with increasing age in the day ($r = -0.694$, $n = 18$, $p < 0.01$) but not the night ($r = -0.033$, $n = 7$, n.s.). The increase of time active during the day (Fig.

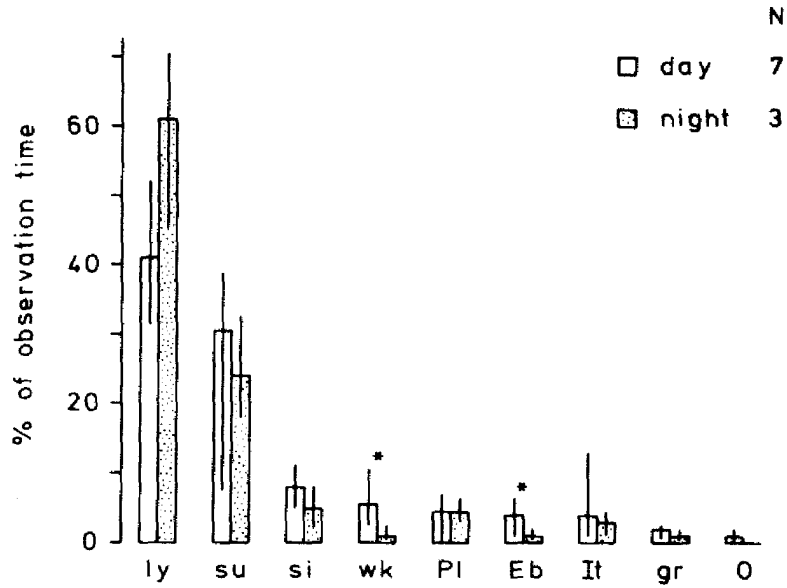


Fig. 5. Proportion of time spent in behavior patterns in the mother's presence (means and ranges for day and night observations). * $p < 0.05$, Mann-Whitney U test, two-tailed.

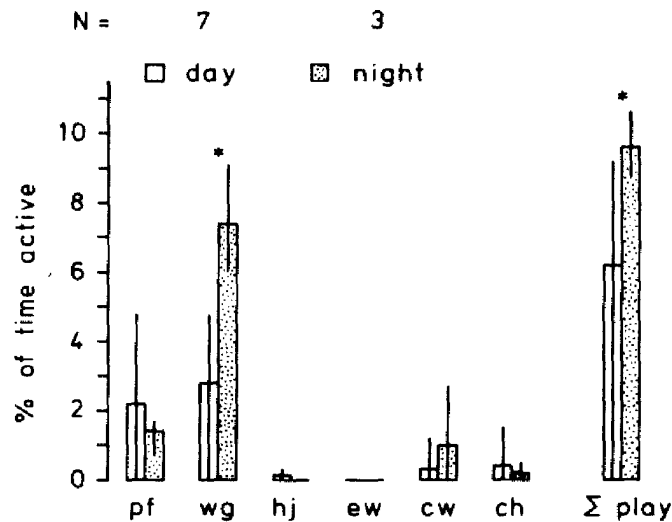


Fig. 6. Differences in play behaviors (in percent of time active) between day and night in the mothers' presence (means and ranges). * $p < 0.05$; Mann-Whitney U test, two-tailed.

3) was therefore produced by a considerable lengthening of activity bouts. The medians of activity bout durations during day and night were not significantly different (day median 76 min, $n = 27$; night median 52.5 min, $n = 8$; Mann-Whitney U test, n.s.).

Differences in day/night occurrence of individual behavior patterns.

During the night pups hardly ever left the immediate proximity of their mothers and never had any opportunity for interactions with other fur seals. The total duration of most behaviors were not significantly different from day to night but exploratory behavior and walking were reduced (Fig. 5). Relative to time active, which was less during the night, a larger proportion of the activity during night-time consisted of play (Fig. 6). This was due to a high incidence of wiggling, which frequently occurred at the end or the beginning of an activity bout.

The mother absent: behavior of pups and sex-differences**Material and methodological considerations**

When the mother was absent, data on pup behavior were recorded between 0600 and 1000 hrs. Two all-day protocols revealed that this was the time of day when pups were most active. Total observation times in the absence of the mother were 66 hrs for 4 male and 12 hrs for 2 female pups. Observed pups were between 18 and 37 days old. These age limits were chosen because pups showed all the behavior patterns studied, from the age of 10 days onwards and did not acquire new ones until their 40th day. Thereafter continuous behavior records were increasingly difficult to obtain as older pups frequently entered the water.

TABLE 1. Observation times (min) on pups in the absence of their mother as distributed over 1st to 4th day of maternal absence

	Day of absence			
	1	2	3	4
Male 1	840	510	515	650
Male 2	—	—	240	—
Male 3	—	720	—	—
Male 4	240	240	—	—
Female 1	240	—	—	—
Female 2	240	240	—	—

Field conditions prevented us from obtaining equal sample sizes of observations on pups of any age or sex category (Table 1). We therefore tested the extent to which individual peculiarities might have influenced results.

Time spent by male pup # 1 in every behavior pattern, as well as his time active during the observation period, were tested against the pooled observations on all other male pups (Mann-Whitney U tests). Statistical significance was not even approached in any of these tests. The ranking of behavior patterns by percentage of time active was the same for all pups (Kendall coefficient of concordance; Chi-square = 144.09, $p < 0.001$, $df = 15$, $K = 13$). Thus it would seem we have recorded a representative sample of pup behavior.

Results

Time active.

Time active and the percentage time of the recorded behavior patterns did not correlate with age (Spearman rank correlations; $p > 0.1$ in all cases; see also Fig. 3). The proportion of time active during our observation interval from 0600 to 1000 hrs remained unchanged up to the 4th day of the mother's absence. If anything there was a tendency to increase time active (Fig. 7). Fig. 7 only shows the data for male pups as just three values were available for female pups. Females appeared to be less active than males; males were active for 138 min (median; range 71-196 min) and females for only 124 min (range 47-125 min) (Mann-Whitney U test, $0.1 > p > 0.05$; $n_1 = 11$, $n_2 = 3$). The duration of the mother's absence had no influence on the length of the activity bouts ($r = 0.354$, $N = 17$, n.s.).

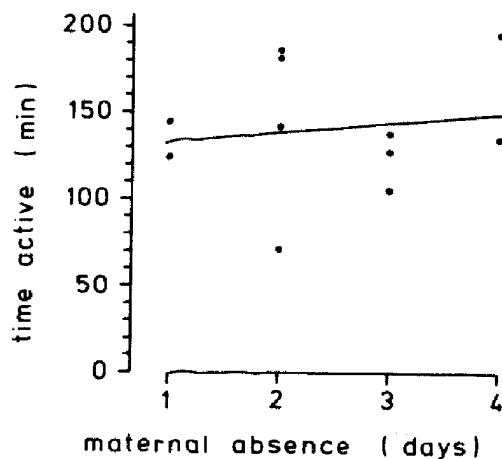


Fig. 7. Time active of male pups during the observation time between 0600 and 1000 hrs plotted against the time the mother had already been absent. Regression: $y = 127.96 + 5.31x$; $r = 0.188$; $n = 11$, n.s.

We observed the first pups born in the reproductive season and although the total number of pups in the area increased as the season progressed this did not influence time active to a substantial degree ($r = 0.320$, $N = 11$, n.s.).

Individual behavior patterns.

Sex differences in pup behavior during the time active were detectable only in play. Females played significantly less than males (Fig. 8). This

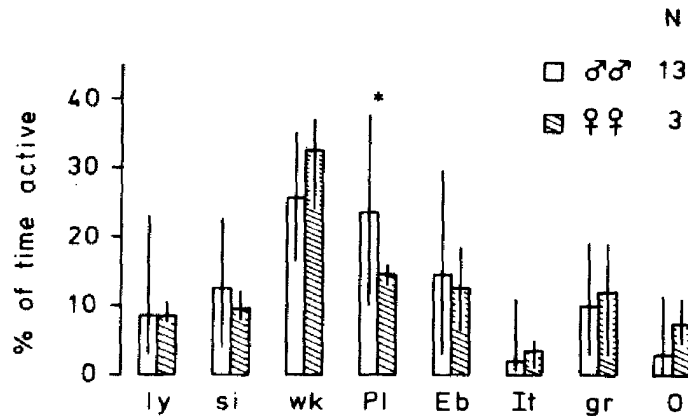


Fig. 8. Sex differences in the proportion of time active spent in different behavior patterns (mean and ranges). Mann-Whitney U test, two-tailed; * $p < 0.05$.

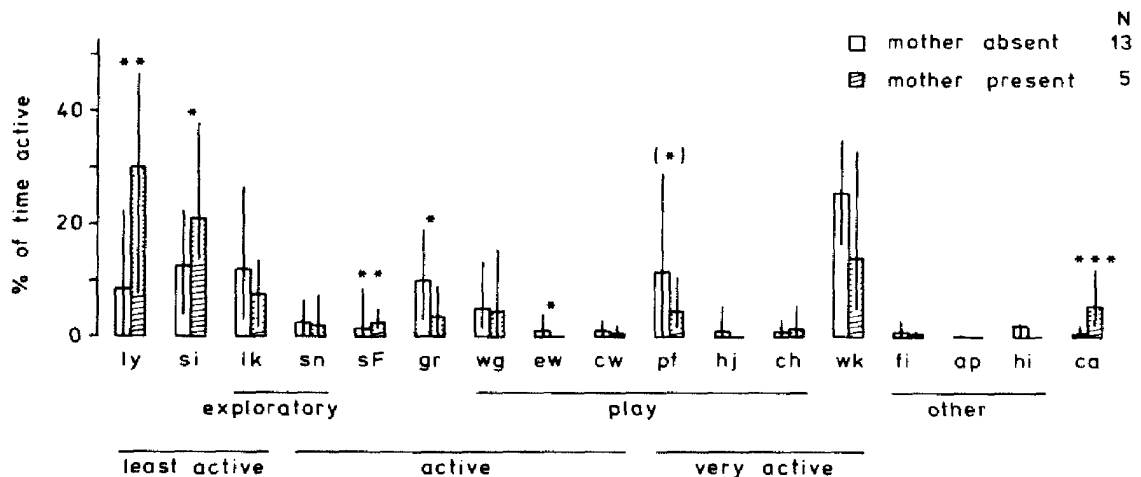


Fig. 9. Proportion of time active spent by males in the various behavior patterns during attendance and absence of the mother. Observation time between 0600 and 1000 hrs; means and ranges are shown. Two-tailed Mann-Whitney U test. *** $p < 0.002$; ** $p < 0.02$; * $p < 0.05$; (*) test on the frequency of play-fighting (see text). Lines on the lower edge of the figure show the grouping of behaviors into higher order categories.

difference was mainly due to play-fighting which lasted almost twice as long in males as in females.

Time spent in each behavior pattern in the mother's absence is shown in Fig. 9. There was no significant correlation between the duration of any behavior pattern and the length of the mother's absence, using Spearman rank correlation coefficients. This was only tested for male pups due to insufficient data for females (the same applies in Fig. 10-12).

The short duration of many of the behavior patterns in Fig. 9 could have obscured negative correlations expected because play should be reduced with increasing hunger of the pup. We therefore tested for changes from highly energetically demanding activities to less demanding ones. Behaviors were grouped into three categories (Fig. 9), each covering roughly equal proportions of the time active:

- 1) least active = ly, si, lk;
- 2) active = gr, wg, sn, sF, ew, and cw;
- 3) very active = wk, pf, hj, and ch.

These categories comprise $96.3 \pm 2.8\%$ of time active in the protocols.

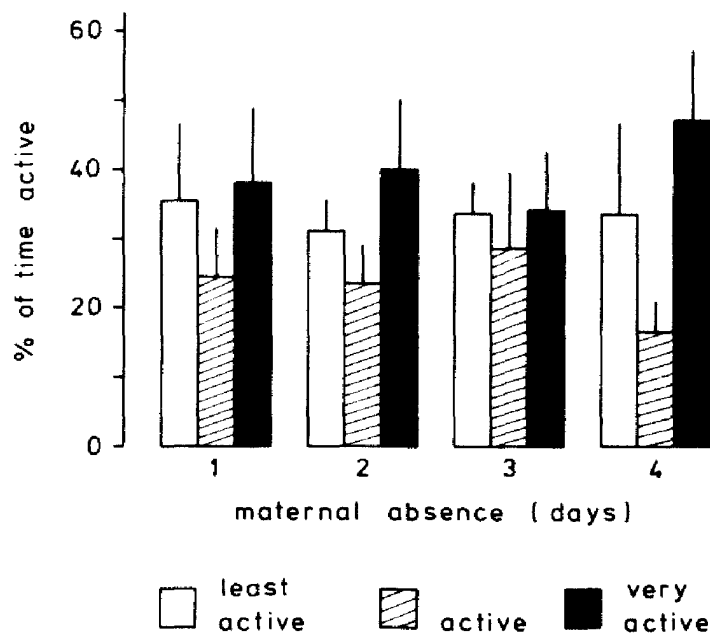


Fig. 10. The proportion of time active spent by males with behaviors in different activity categories (compare Fig. 9) plotted against the duration of maternal absence. Means and standard deviations. Kendall's coefficient of concordance: very active > least active > active, $p < 0.01$; $K = 13$; $n = 3$.

Fig. 10 shows the proportions of the three categories against duration of the mother's absence. "Very active" behaviors were always highest, followed by "least active" and "active" ones (Kendall coefficient of concordance, $p < 0.01$). If the length of the mother's absence had a negative influence on the activity of her pup one would expect an increase of "least active" or "active" behaviors at the expense of "very active" ones as total activity always remained approximately the same (Fig. 7). The values of the "very active" behaviors on the third and fourth day of

the mother's absence were stepwise decreased by 0.5% to test the sensitivity of the Kendall coefficient of concordance to small changes. A decrease of only 3 percent in the category "very active" destroyed the significance of the Kendall coefficient of concordance, regardless of how this 3 percent was distributed between the other 2 categories.

This analysis shows that the behavior of pups remained uninfluenced by even a 4 day absence of the mother.

Differences in pup behavior in the presence and absence of the mother.

Pups were more active in the presence than in the absence of their mothers (Fig. 11). This difference was caused by long suckling times. Time active without time suckling was rather less in the presence than in the absence of the mother.

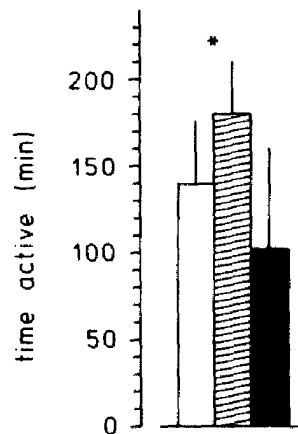


Fig. 11. Time active during the total observation time between 0600 and 1000 hrs in the mothers' presence and absence (males only; means and standard deviations). Mann-Whitney U test, two-tailed; * $p < 0.05$. Open bar: mother absent; hatched bar: mother present, suckling time included; black bar: mother present, suckling time excluded.

Activity bouts appeared to be slightly shorter when the mother was absent but this was not significant (Mann-Whitney U test, two-tailed; mother present $n = 27$, mother absent $n = 16$; n.s.). The same result was obtained when suckling was not included in the calculation of activity bout length.

With reference to total observation time lone pups clearly played and groomed more and showed less calling and sniffing at other fur seals which is performed mostly with the mother (Fig. 12). "Hidden" observa-

tions also occurred more frequently in the absence of the mother as pups moved further when alone and were therefore more difficult to observe.

Behavior during the time active.

Differences in pup behavior during their time active in the absence and presence of the mother were examined by calculating the percentage of time spent in each behavior pattern excluding suckling (Fig. 9). Less energetically demanding behaviors like sitting and lying predominated in the mother's presence, while walking and play behaviors occurred less, although these trends were not significant. The decrease in play behavior was mainly due to less play-fighting in the presence of the mother. This result is not significant in a comparison of time budget data ($0.1 > p > 0.05$) but becomes so ($p < 0.05$) when the frequencies of play fighting with and without the mother in attendance are compared.

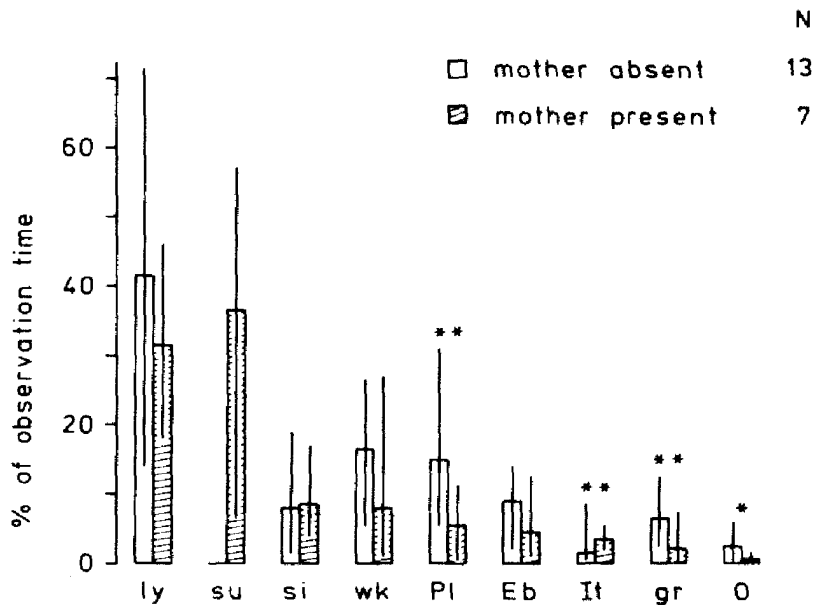


Fig. 12. Proportion of observation time spent by males in various behavior patterns (means and ranges). Mann-Whitney U test, two-tailed; ** $p < 0.02$; * $p < 0.05$.

Time spent play-fighting correlated positively with time when opportunity for contact existed ($p < 0.05$, $r_s = 0.829$, $n = 6$). A pup's only opportunity to contact other pups came when its mother was absent or when it separated from the mother, as mothers were always quite aggressive towards strange pups. This lowered the pups' opportunities for interaction significantly (mother present *versus* mother absent $p < 0.05$).

In the mother's absence, total time with opportunities for contact did not correlate significantly with the number of pups in the study area ($r_s = -0.435$; $n = 6$; n.s.).

Discussion

Stability of activity and play under conditions of varying food intake.

The pups' activity budget was largely independent of their mothers' attendance-absence cycle: they were always active for about 60% of the time (Figs 3 and 7). This was so despite the mothers spending 63% of their total time in 1980 at sea and only 48% away in the food-rich year 1981 (TRILLMICH, in press). Of course at some point the food deficit will become so large as to force changes in a pup's activity budget. The time span necessary to create this effect must be much longer than the average absence duration. The critical low set-point for body reserves could best be detected in pups losing their mothers and thus exposed to continuous starvation. A starving pup only a few days old demonstrated the eventual end point in reduction of activity: during a continuous 12 hr observation it only showed the activity necessary for behavioral thermoregulation and did not play at all.

Play is one of the most energetically demanding activities of young (COELHO, 1974; COELHO *et al.*, 1976). Nevertheless the short activity bouts, typical for play, increase total daily energy expenditure only slightly. However, under conditions of reduced energy input the cost of additional activity may show in a weight reduction or decreased growth (MARTIN, 1982). Fur seal pups lived on their energy reserves while their mothers were at sea (Fig. 1). In this situation growth and activity, including play, necessarily compete for limited body reserves, but the storage of a large amount of energy in the blubber layer apparently permits the pups to maintain more or less constant levels of activity and play.

However, when the mother returned and food uptake became possible, sucking and digestion had high priority (Fig. 12). Walking, playing, looking around and grooming were reduced and during time active the less energetically demanding activities like lying and sitting predominated (fig. 9). Total activity of pups, excluding sucking, also seemed to be lessened in the mothers' presence (Fig. 11) and pups played less than when alone.

The maintenance of a high level of activity and play during the prolonged absence of the mother is hard to understand in the framework of the traditional assumption of a fixed motivational system with play on one of the lowest ranks in the hierarchical order (MEYER-HOLZAPFEL, 1956; BALLY, 1966; HINDE, 1973; EIBEL-EIBESFELD, 1980). A pup is exposed to increasing hunger and perhaps thirst when deprived of food due to the mother's absence. Nevertheless, this did not reduce activity or play, thus indicating that play is a high ranking activity well able to compete with other behavioral tendencies. Food uptake seems to have highest priority in Galapagos fur seal pups only when the mother is present. In her absence, however, a strong play tendency ensures that play remains at a relatively high level, as no behavioral alternatives like milk stealing or independent foraging are available.

A comparison of our data with results from other species suggests that the behavioral ecology of a given species greatly influences the relative behavioral dominance of the play motivation. Young White-tailed deer react very quickly with a reduction of play activity when deprived of food (MÜLLER-SCHWARZE *et al.*, 1982). The young in the field are fed or feed themselves at short intervals and at an early age milk ceases to be their main energy source. They can feed themselves by increasing the time spent grazing or browsing instead of playing. Young fur seals, however, do not have this option.

Potential benefits and costs of play for fur seals.

Maintaining a constant level of activity and play in the mothers' absence will only be favored by selection if pups benefit from their activities. One possible benefit accrues mostly to male pups. Reproductive success of a fur seal male depends mainly on his ability to establish and defend a territory. Fighting success is largely determined by size and strength but also depends on fighting tactics. Males can sometimes displace larger opponents if, by quick manoeuvring, they can land a serious bite at the head or foreflippers. Play-fighting supposedly develops manoeuvring powers and fighting strategies so it is bound to be very beneficial in later life.

One further direct benefit of play interactions between pups may lie in the establishment of a (site specific?) dominance hierarchy. Pups thus appear to ensure preferential access to their individual resting sites in the shade.

Play-fighting, chasing and similar strength and agility increasing actions are not the only behaviors which seem beneficial for pups: even

looking, for example, may train their information processing systems. Fur seals often scan the environment behind themselves by raising the head until the snout points straight upwards or slightly backwards. This produces an inverted image on the retina. Pups show this behavior, included in our definition of looking, very often. During play they even look at objects in front of them by turning the head around the longitudinal axis until the same effect results. This behavior must provide considerable practice in recognizing objects irrespective of their orientation on the retina: a very useful ability later on when young seals must learn to find and identify prey while diving in their three-dimensional marine environment.

Besides its immediate energetic costs, play activity increases the risks of separation from the mother and of injury. Very young pups may be washed out to sea when playing near the water. If they are displaced far from the usual mother-pup reunion site they may become permanently separated and starve to death. Play activity increases the risk of falling into holes and crevices from which pups may be unable to escape. One to 5% of the pups die every year in such accidents (TRILLMICH, 1981). Furthermore, playing pups often inadvertently approach too close to strange females precipitating attacks which can be dangerous.

Sex differences.

FAGEN's (1981, Chapter 6) model of play behavior predicts sex correlated differences in the amount of play activity for sexually dimorphic species. While females may successfully reproduce without much play experience, males presumably have to develop their competitive abilities through intensive play behavior.

Male Galapagos fur seal pups seemed to be more active than females and played more, even relative to time active (Fig. 8). The increase in activity with age (Fig. 3) appeared, in male pups, to be accompanied by augmented weight loss while females showed the opposite trend (Fig. 2). This suggests that males spend increasingly more energy on activity than do females.

The sex differences in the behavior of Galapagos fur seal pups appeared to be less pronounced than those GENTRY (1974) found in Steller sea lions (*Eumetopias jubata*). He describes a clear sexual dimorphism for most behavior patterns occurring in play bouts of Steller sea lion pups of approximately the same age as our fur seals. Male Steller pups showed five times as much play-fighting as females but there was only a non-

significant tendency in the same direction in Galapagos fur seal pups. A reduced sex difference in the occurrence of play behavior might correspond to the diminished sexual dimorphism in the Galapagos fur seal (TRILLMICH, 1984).

Summary

Time budgets of Galapagos fur seal pups were recorded. Two male pups were observed between the ages of 1 and 60 days, when their mothers were ashore. They became more active as they grew older and always showed more activity during the day than at night. Four male and 2 female pups, aged between 18 and 37 days, were observed in the absence of their mothers. The influence of age on activity level could be discounted during this period. Pups did not forage independently and therefore continuously lost weight while their mothers were at sea for a maximum of 4 continuous days; nevertheless, the pups' activity level remained constant.

Pups were active for more time in the mother's presence than in her absence. But this was only due to long sucking times. Otherwise, less energetically demanding activities like sitting and lying predominated during the time active and playing and walking appeared to be reduced in the mother's presence.

Male pups seemed to be more active than female pups, particularly in play-fighting. As they grew older, male pups lost more weight per unit time in the mothers' absence than female pups.

The maintenance of a high level of activity and play in the mothers' absence, despite a lack of energy intake, can be explained by the behavioral ecology of fur seals. Benefits and costs as well as sex differences of play behavior are discussed.

References

- ALTMANN, J. (1974). Observational study of behavior: sampling methods. — *Behaviour* 49, p. 227-267.
- BALDWIN, J. D. & BALDWIN, J. I. (1972). The ecology and behavior of squirrel monkeys (*Saimiri oerstedii*) in a natural forest in western Panama. — *Folia Primatol.* 18, p. 161-184.
- (1976). Effects of food ecology on social play: a laboratory simulation. — *Z. Tierpsychol.* 40, p. 1-14.
- BALLY, G. (1966). Vom Spielraum der Freiheit. Die Bedeutung des Spiels bei Tier und Mensch. — Verlag Schwabe, Basel.
- BONNER, W. N. (1981). Southern fur seals *Arctocephalus* (Geoffroy Saint-Hilaire & Cuvier, 1826). — In: Handbook of marine mammals, Vol. 1 (RIDGWAY, S. H. & HARRISON, R. J., eds). Academic Press, London 1981, p. 161-208.
- COELHO, A. M. (1974). Socio-bioenergetics and sexual dimorphism in primates. — *Primates* 15, p. 263-269.
- , BRAMBLETT, C. A., QUICK, L. B. & BRAMBLETT, S. S. (1976). Resource availability and population density in primates: A socio-bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. — *Primates* 17, p. 63-80.
- DASMAN, R. F. & TABER, R. D. (1956). Behavior of Columbian black-tailed deer with reference to population ecology. — *J. Mammal.* 37, p. 143-164.
- EIBL-EIBESFELD, I. (1980). Grundriss der vergleichenden Verhaltensforschung. — Piper und Co., München.
- FAGEN, R. (1981). Animal play behavior. — Oxford University Press, New York.

- GEIST, V. (1971). Mountain sheep: A study in behavior and evolution. — University of Chicago Press, Chicago.
- GENTRY, R. L. (1974). The development of social behavior through play in the Steller sea lion. — *Am. Zool.* 14, p. 391-403.
- (1981). Northern fur seal *Callorhinus ursinus* (Linnaeus, 1758). — In: Handbook of marine mammals, Vol. 1. (RIDGWAY, S. H. & HARRISON, R. J., eds). Academic Press, London, 1981, p. 143-160.
- HINDE, R. A. (1973). Animal behaviour. — McGraw-Hill, New York.
- LOY, J. (1970). Behavioral responses of free-ranging rhesus monkeys to food shortage. — *Am. J. Physiol. Anthropol.* 33, p. 263-271.
- MARTIN, P. (1982). The energy cost of play: definition and estimation. — *Anim. Behav.* 30, p. 294-295.
- MEYER-HOLZAPFEL, M. (1956). Über die Bereitschaft zu Spiel- und Instinkthandlungen. — *Z. Tierpsychol.* 13, p. 442-462.
- MILLER, E. H. (1975). A comparative study of facial expressions of two species of pinnipeds. — *Behaviour* 53, p. 268-284.
- MÜLLER-SCHWARZE, D., STAGGE, B. & MÜLLER-SCHWARZE, C. (1982). Play behavior: persistence, decrease, and energetic compensation during food shortage in deer fawns. — *Science* 215, p. 85-87.
- RICHARD, A. F. & HEIMBUCH, R. (1975). An analysis of the social behavior of three groups of *Propithecus verreauxi*. — In: Lemur biology (TATTERSALL, I. & SUSSMAN, R. W., eds). Plenum Press, New York, 1975, p. 313-333.
- ROSENBLUM, L. A., KAUFMAN, I. C. & STYNES, A. J. (1969). Interspecific variations in the effects of hunger on diurnally varying behavior elements in macaques. — *Brain, Behav. Evol.* 2, p. 119-131.
- RUTISHAUER, I. H. E. & WHITEHEAD, R. G. (1972). Energy intake and expenditure in 1-3 year old Ugandan children living in a rural environment. — *Br. J. Nutr.* 28, p. 145-152.
- SCHALLER, G. B. (1972). The Serengeti lion. — University of Chicago Press, Chicago, 1972.
- (1977). Mountain monarchs: wild sheep and goats of the Himalaya. — University of Chicago Press, Chicago, 1977.
- SOUTHWICK, C. H. (1967). An experimental study of intergroup agonistic behavior in rhesus monkeys (*Macaca mulatta*). — *Behaviour* 28, p. 182-209.
- TRILLMICH, F. (1981). Mutual mother-pup recognition in Galapagos fur seals and sea lions: Cues used and functional significance. — *Behaviour* 78, p. 21-42.
- (1984). Natural history of the Galapagos fur seal (*Arctocephalus galapagoensis*, Heller). — In: Key environments: Galapagos (PERRY, E., ed.). Pergamon Press, Oxford, 1984, p. 215-223.
- (in press). Attendance behavior of Galapagos fur seal females. — In: Fur seals: Maternal strategies on land and at sea (GENTRY, R. L. & KOOYMAN, G. L., eds). Princeton University Press, Princeton.
- & MOHREN, W. (1981). Effects of the lunar cycle on the Galapagos fur seal, *Arctocephalus galapagoensis*. — *Oecologia* 48, p. 85-92.
- ZIMMERMANN, R. R., GEIST, C. R. & ACKLES, P. K. (1975). Changes in the social behavior of rhesus monkeys during rehabilitation from prolonged protein-calorie malnutrition. — *Behav. Biol.* 14, p. 325-334.

Zusammenfassung

Von jungen Galapagos Seebären wurden Aktivitätsbudgets erstellt. Bei Anwesenheit der Mutter wurden 2 Männchen zwischen dem 1. und 60. Lebensstag beobachtet. Sie wurden mit zunehmenden Alter aktiver, die Tagesaktivität lag dabei immer in gleichem Maße über der Nachtaktivität.

Die während der Abwesenheit der Mutter beobachteten Tiere (4 Männchen, 2 Weibchen) waren zwischen 18 und 37 Tagen alt. Ein Einfluß des Lebensalters auf die Aktivität konnte in diesem Zeitraum vernachlässigt werden. Während der maximal 4-tägigen Abwesenheit der Mutter verloren die Jungtiere ständig an Gewicht, da sie keinerlei Gelegenheit zur selbständigen Nahrungsaufnahme hatten. Trotzdem blieben sie über den gesamten Zeitraum unverändert aktiv.

In Anwesenheit der Mutter waren die Jungtiere mehr Zeit aktiv als in ihrer Abwesenheit. Dies war jedoch allein auf den hohen Anteil der Trinkzeit zurückzuführen. Ansonsten überwogen die energetisch weniger aufwendigen Verhaltensweisen wie Sitzen und Liegen in der Aktivitätszeit. Laufen und Spiel waren eher reduziert.

Männchen schienen insgesamt aktiver zu sein als Weibchen. Deutlich war dies beim Kampfspiel zu sehen. Männchen nahmen während der Abwesenheit der Mutter mit zunehmendem Lebensalter auch stärker ab als Weibchen.

Warum ein bestimmtes Aktivitäts- und Spielniveau trotz langer Unterbrechung der Energiezufuhr aufrechterhalten wird, kann im Zusammenhang mit der Verhaltensökologie der Seebären verstanden werden. Nutzen und Kosten sowie Geschlechtsunterschiede des Spielverhaltens werden diskutiert.