Maternal and Paternal Care in the Rock Cavy, *Kerodon rupestris,* a South American Hystricomorph Rodent

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The maternal and paternal behavior of *Kerodon rupestris* was examined. Quantitative differences between fathers and mothers and between mothers raising young with fathers present and with fathers absent were assessed. Growth rates of young raised by paired females and by lone females were compared.

The male provides direct paternal care to the young by engaging in allogrooming, sniffing, and huddling. There is no significant difference between the sexes in the amount of contact promoting behavior given to the offspring, nor are the sexes significantly different in the amount of exploratory sniffing of the offspring. When the male is absent, the female spends a greater amount of time in contact with the young. Young raised by lone females gained significantly more weight than young raised by paired females.

The suggestion that indirect paternal care acts to reduce female aggression to the young and relieve the energy expenditure burden of the female is discussed. The results indicate that social experience is gained at the expense of physical nurturing when the male is present.

Key words: parental behavior, parental care, maternal behavior, paternal behavior, rodent, rock cavy

INTRODUCTION

A common form of social organization in rodents consists of 1) male and female pairing for copulation, 2) pair separation, 3) parturition and female nest defense, 4) association between the female and the litter, and 5) dispersion of the litter [Eisenberg, 1963]. For any species, its social structure is the result of the quantity and quality of agonistic behavior, courtship behavior, and aid-related behavior [Brown, 1975]. Included in aid-related behavior is parental care, the study of which is one means of retrieving information about social organization [Eisenberg, 1963].

The rodents are divided into three suborders based on skull shape and the attachment and strength of the jaw muscle: the squirrel-like Sciuromorpha, the mouse-like Myomorpha, and the porcupine-like Hystricomorpha (Landry, 1957). The Hystricomorpha are of interest because they differ in some ways from the basic myomorph patterns of behavior, although they have radiated into a variety of habitats. Among the behaviors that have been modified is parental behavior, because of the physiological adaptations of lengthened gestation period, smaller litter size, and precocial neonates [Kleiman, 1974; Kleiman et al, 1979].

In the past, studies of parental care in rodents had concentrated on maternal contributions [Rheingold, 1963]. Recent research has shown that the male of some species does influence ontogeny of the young.

In this paper the terms "care" and "investment" are used interchangeably and refer to any behavior directed toward an offspring that increases the offspring's chance of survival [Trivers, 1972]. The parent determines for its young the physical environment—the nesting site and movement in, around, and away from that site—as well as the social environment—the amount and kinds of contact with members of the species [Rheingold, 1963].

Three determinants of the amount of paternal care rendered are mating systems, female receptivity to the male, and male association with the young. Paternal investment is expected to be greatest among species exhibiting monogamy, stable harem situations, or social pair bonding in which the parents remain closely associated postpartum [Kleiman, 1977]. In hystricomorph rodents, estimates are that at least 70–75% of the species are colonial, communal, or pair-bonded outside a reproductive context. In these social units the males are frequently exposed to their own offspring. It is instructive to ask, then, to what extent and in what mode does the male contribute to care of the young?

The rock cavy, *Kerodon rupestris* represents a good model for the study of biparental care. *Kerodon* is a monospecific hystricomorph rodent genus of the family Caviidae. The caviids are divided into two subfamilies, the harelike Dolichotinae, and the guinea pig-like Caviinae. *Kerodon* belongs to the Caviinae along with three other genera, *Cavia* (guinea pig), *Galea* (cuis), and *Microcavia* (desert cavy). While the other genera have a broad distribution throughout South America and may be found in sympatry in parts of Argentina [Rood, 1972], *Kerodon* is a habitat specialist limited to the semiarid Caatinga of northern Brazil [Walker, 1968].

As far as is known to the present author, the only research conducted on *Kerodon* suggests that captive and wild colonies practice a mating system of resource-defense polygyny (Lacher, 1980]. Lacher indicates that males vie for rock piles. Females then select the rocks and indirectly choose the male. As a result, males, females, and young remain in close association, and parental care might be predicted to involve both the mother and the father. Because *Kerodon* breed well as pairs in captivity, there is an opportunity to study biparental care in this species.

Current research has shown considerable paternal care in the three mammalian orders Carnivora, Primates, and Rodentia [Kleiman and Malcolm, 1980]. Most information on male behavior toward young rodents is from the suborder Myomorpha [Spencer-Booth, 1970].

Males of several species have been shown to have an effect on ontogeny of young. For example, growth and activity differ in *Mus musculus* young reared by a male and female relative to young reared by two females [Smith and Simmel, 1977; Fullerton and Cowley, 1971]. Male southern grasshopper mouse pups, *Onychomys*

torridus, showed increased interspecific aggression when reared in the father's presence as compared to the behavior of female-reared male pups [McCarty and Southwick, 1977b]. Male *Peromyscus leucopus*, white-footed mice, are reported to give considerable care to their offspring [Spencer-Booth, 1970]. Horner [1947] gave the first account, in anecdotal form, of licking and retrieval behavior by males of this genus. A study of *P. californicus parasiticus* that compared the effects of housing pups with and without the father and/or temporary removal of the mother demonstrated that pups were heavier during early development when the male was present [Dudley, 1974a]. Elwood [1975] indicates that in *Meriones unguiculatus*, the Mongolian gerbil, all "maternal" activities, excluding nursing, are performed by both sexes, revealing that paternal investment is an integral part of raising the young. Both parents contribute equally in *Microtus ochrogaster*, the prairie vole [Thomas and Birney, 1979]. Paternal care in some form is also found in *Baiomys taylori* (pygmy mouse), *Lemmus lemmus* (lemming), *Reithrodontomys humulis* (eastern harvest mouse) [Spencer-Booth, 1970], and *P. leucopus* [McCarty and Southwick, 1977a].

Within the Sciuromorpha, paternal care is not seen in *Tamiasciurus* (red squirrels), *Glaucomys volans* (southern flying squirrel), or some species of *Marmota* [Spencer-Booth, 1970]. Members of the family Heteromyidae lead a solitary existence, with adults coming together only for breeding purposes [Eisenberg, 1963]. In comparison, the beaver, *Castor fiber*, practices monogamy, and the male is an integral part of the family and aids in rearing young [Kleiman, 1977].

The suborder Hystricomorpha is the least studied with respect to paternal care, but the male is known to be tolerant toward the young in *Capromys* (long-tailed hutia) and *Octodon* (South American bush rat) [Kleiman, 1974]. Males of *Myoprocta pratti* (green acouchi) have been observed to carry nest materials to the site where offspring are located [Kleiman, 1977]. Also, they have frequently been seen sleeping with and licking the young [Kleiman, 1972]. Survival of young was highest among groups raised with *M. pratti* males and females; cannibilism occurred when solitary females raised young [Kleiman, 1970].

To date, studies of the Caviianae have been sparse in regard to paternal behavior. One study, in which male *Cavia porcellus* were made to lactate by castration and implantation of ovaries, reports that males refused to nurse young that had been removed from their mother a few days after birth [Nelson and Smelser, 1933]. Another reports a polygynous group of *C. porcellus* in which the male was tolerant of the young but offered no care [King, 1956]. Because this species is domesticated, the behavior may differ from that of related wild species [Hale, 1962].

Comparative studies have been useful in understanding the evolution of social behavior and the extent of its lability [Eisenberg, 1967]. Behavioral repertories for all caviine genera have now been completed, but taxonomic relationships are still not clear [Rood, 1972; Lacher, 1980]. In the present study, parental behavior in *Kerodon* is examined and differences between males and females are quantified. The expression of maternal behavior when the father is not part of the family group is also quantified.

METHODS

The subjects of the present study were five female and five male rock cavies, *Kerodon rupestris* (Table 1). They were maintained by the Department of Zoological Research at the National Zoological Park (NZP), Washington, DC. With the excep-

TABLE 1. Family Unit Compositions for the Study of Maternal and Paternal Care in *Kerodon rupestris*.

| Unit No. (date established) | Subjects | | | | No. litters prior study |
	Accession No.	Sex	House ID	Ear tag ID	
1(5/19/78)	102348	F	7	Left blue	5
	102344	M	3	Right orange	
2(5/19/78)	102349	F	8	Left red	4
	102346	M	5	Right green	
3(5/19/78)	102350	F	9	Left green	4
	102345	M	4	Right orange	
4(5/19/78)	102351	F	10	Left orange	2
	102347	M	6	Right red	
5(2/27/79)	102521	F	14	No tag	1
	102342	M	1	Right red	

tion of one female, the animals were caught wild in Brazil and received by NZP on May 19, 1978. Female 14 was born captive on August 24, 1978, to female 7 and male 3. Male and female subjects were paired upon arrival forming breeding units, except unit 5, which was paired on February 27, 1979. All subjects had bred and reared at least one litter in captivity prior to the present study. The animals were ear-tagged on January 25, 1979, using a color coding system to facilitate individual identification. Formal observations were begun on May 21, 1979, and concluded on November 26, 1979.

Each unit was housed in either a steel cage (120 cm^3) or a wooden frame cage with hardware cloth (180 × 180 × 210 cm). Wood shavings and hay were used for substrate. Several wooden shelves and/or branches were arranged as runways and perches. Each cage contained a wooden nest box (22 × 45 × 22 cm) constructed with a transparent plastic window to allow unobstructed viewing of nest box activity. Cages were cleaned twice weekly. Diet, consisting of kale, maple leaves (*Acer* sp.), grain mix (sunflower seeds, commercial rabbit pellets, scatch feed, raw peanuts), raw fruits and vegetables, and water, was supplied ad lib. The temperature was maintained at 20–27°C. A 12-h light, 12-h dark cycle was used, with a dark phase from 1500 h to 0300 h. Observations were made randomly between 1100 h and 1900 h while the observer was seated approximately 6 feet from the cage. During observations made in the dark phase, two 7.5-W "moonlight" bulbs were used on the cage. These lights were turned off at the end of each "dark" observation session. *Kerodon* are apparently active throughout the day, with a slight depression in activity level during the midday hours [Lacher, 1980].

Two consecutive litters per unit were observed under two parental environments. The first litter was removed from the unit about 2 weeks prior to the birth of the second litter. One litter was reared by both female and male parents; the other litter was reared by the female parent only. The determination of which parental environment was observed first was randomly assigned for each unit.

Kerodon possess a vaginal closure membrane, a characteristic typical of hystricomorphs. The vaginal closure membrane usually seals the vagina quickly once mating has occurred, but its closing may be delayed after parturition. There is usually a postpartum estrus. The shortest interval between litters is usually taken to be the

gestation period [Weir, 1974]. To take advantage of the postpartum estrus, males remained with their female mates for 3 days following parturition and were subsequently removed for the female only parental environment. In all cases, therefore, observations began 4 days after birth and continued on alternate days until day 50.

Observations were made of each female in two parental conditions, with and without males. Males were observed in the paired condition. Therefore, for every unit, three conditions were generated: 1) F+ (paired female), female rearing young with the male present; 2) F− (lone female), female rearing young with the male absent; and 3) M, male rearing young with the female present. For statistical purposes, the 24 observation days (day 4 to day 50) were divided into three equal time periods—period I (day 4 to day 18), period II (day 20 to day 34), and period III (day 36 to day 50). A check sheet was employed for data collection. Each parent was used as a focal subject. The focal subject was that animal through which all observations of behaviors affected by or affecting that animal were interpreted [Altmann, 1974]. Observation sessions were 30 min with each minute divided into four 15-sec intervals. This allowed for the recording of both states and events, which were measured by duration and frequency, respectively [Altmann, 1974].

Behaviors examined in this study (Table 2) were derived from Rood [1972] with the following additions and/or changes: "nose-rear" (termed nasoanal by Rood) was

TABLE 2. Kerodon Behaviors Used for the Present Study, Based on 30-Min Observation Sessions, Divided Into 15-Sec Intervals

Behavior category	Behavior	Form of data collection
States		
Huddling	One-parent huddle [Hud (1)]	Duration
	Two-parent huddle [Hud (2)]	Duration
Nursing	Nurse [Nvr]	Duration
	Initiation	Frequency
Total contact time	M: Hud (1) + Hud (2) − (M)	Duration
	F+: Hud (1) + Hud (2) + Nur (F+)	Duration
	F−: Hud (1) + Nur (F−)	Duration
Courtship		Duration
Events		
Social	Nose-nose	Frequency of occurrence
Exploratory sniffing	Nuzzle	throughout 30-min
	Nose-rear	observation
Contact-promoting	Climb over	
	Crawl under	
	Allogroom	
Aggressive	Head lunge	Frequency of occurrence
	Bite	throughout 30-min
	Chase	observation
Maintenance	Rest	Frequency at 15-sec
	Locomote	intervals; one of the
	Autogroom	five is always
	Forage	performed
	Gnaw	

defined as a contact-promoting behavior, not a sexual pattern; "nose-nudge" occurred when an animal pressed its nose against another's body (usually in the flank or midventer region) in an attempt to move that animal to a more desired position—eg, young to female in suckling, parent to young in huddling, male to female in courtship pursuit; "bite" was a high-intensity head lunge in which the attacker gave or attempted a quick nip to the recipient.

Huddling and nursing were mutually exclusive states scored for duration with a possible maximum of 1,800 sec. Huddling was broken down to two subcategories—type 1, a huddle consisting of one parent and at least one of the young, and type 2, a huddle consisting of both parents and at least one of the young. In this study, analysis of huddle refers to type 1 single-parent huddling. This enabled comparisons of F+ and F−. For a more complete measure of time spent with the offspring by a parent, the category "total contact time" was created. This was the sum of type 1 and type 2 huddling, plus nursing, where applicable.

When discernible, nursing initiation was recorded. "Female-initiated" nursing was recorded when nursing ensued after the female approached the young or exposed her nipples as a consequence of a posture shift. "Young-initiated" nursing was scored if nursing followed as a result of offspring climbing over, crawling under, or nose-nudging the mother to expose a nipple.

Because social and aggressive events occurred infrequently, total frequencies for the entire observation session were recorded. Unlike maintenance behaviors (see below), no maximum frequency limit was imposed by the design.

Maintenance behaviors occurred independently of all other behaviors, and one of five events was always checked off after a 15-sec interval. Thus for any maintenance behavior, a maximum of 120 counts could be obtained. Resting, a maintenance behavior, was scored during inactivity (eg, sitting and lying) as well as during stationary social behaviors such as allogrooming and nursing.

An additional behavior included courtship, a state exclusive of all other duration behaviors. The following activities were recorded as courtship behavior: foot tapping, nose-rump following, circling, mounting, and straddling. Comments on ontogeny were also recorded.

The animals were not handled in this study except to obtain weight measurements. Females were weighed biweekly to monitor pregnancy. Offspring were weighed after every observation session to collect data for growth rates.

RESULTS
Behavior States: Total Contact Time, Huddling, Nursing

The results of two-way analyses of variance for behavior states are summarized in Table 3. Significant interaction effects were found for nursing. The presence of the interaction makes it impossible to examine the independent effects of time and parental type for this behavior. Nursing interaction effects will be reviewed subsequent to the other duration behaviors. Least-significant difference (LSD) tests at the $P \leqslant 0.05$ significance level were performed and confidence intervals are shown in Figures 1–3. Nursing behavior was treated with an LSD test with Tukey's modification for comparison among means [Snedecor and Cochran, 1967].

Differences in total contact time were significant in all parental-type conditions but only approached significance in time-period effects. Overall, lone females spent

more time with the young than did the paired females (over 1.5-fold), and the paired females spent more time with the young than did the males (nearly 2-fold) (Fig. 1).

Lone females huddled with their offspring significantly more than did paired females (nearly 4-fold), although no significant time-period effect was found. Similarly, paired females huddled with their young significantly more than did males (over 2-fold), but time-period differences were not significant (Fig. 2).

Figure 3 shows interaction effects of nursing behavior for F+ and F− over the three time periods. No significant difference in mean time spent nursing was found during periods I and III, whereas the paired females nursed almost four times as much as the lone females during period II. No nursing was observed for any case by the last day of period III.

Gestation, Litter Size, and Growth Rate

Table 4 shows birth dates of offspring, estimated gestation periods, and litter size for animals used in the present study. The mean gestation period was 75.9 ± 1.14 SE days, and the mean litter size was 1.58 ± 0.73 SE animals.

Linear regression analyses of weight gains against time were made for young of both F+ and F− conditions (Fig. 4). Not surprisingly, in both cases, weight gain was strongly correlated with an increase in age (r = 0.93 for F+; r = 0.85 for F−). Another source [Lacher, 1979] reports that this trend continued until day 120, when

TABLE 3. Results of Two-Way Analyses of Variance for Behavior States

| Variation	Sum of squares	df	Mean square	F	P <
Total contact time F+, F−					
Parental type	11577312	1	11577312	26.829	0.001
Time period	1734702	2	867351	2.010	0.134
Interaction	2271035	2	1135517	2.631	0.072
Error	100975749	234	431520		
Total contact time F+, M					
Parental type	5615406	1	5615406	13.812	0.001
Time period	2322395	2	1161197	2.856	0.058
Interaction	1888899	2	944449	2.323	0.098
Error	95138334	234	406574		
Huddling F+, F−					
Parental type	33550794	1	33550794	126.808	0.001
Time period	778588	2	389294	1.471	0.230
Interaction	461439	2	230719	0.872	0.999
Error	61911397	234	264578		
Huddling F+, M					
Parental type	1297275	1	1297275	11.915	0.001
Time period	135388	2	67694	0.622	0.999
Interaction	459340	2	229670	2.109	0.121
Error	25476838	234	108875		
Nursing F+, F−					
Parental type	1331762	1	1331762	14.175	0.001
Time period	1470937	2	735468	7.828	0.001
Interaction	653523	2	326761	3.478	0.032
Error	21984400	234	93950		
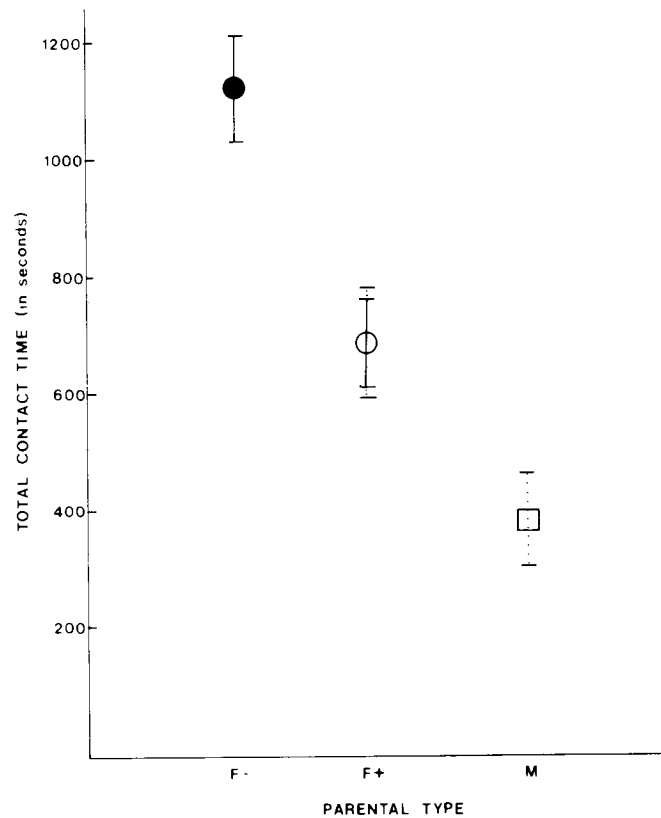
Fig. 1. Mean total contact time of parental types per 30-min session over total observation time. Ninety-five percent least-significant confidence intervals (LSCIs) are placed about the mean values. Dotted lines represent LSCIs for F+ and M comparisons. Solid lines represent LSCIs for F+ and F− comparisons. Solid circle, F−, open circle, F+, open square, M.

the rate began to decrease and weights began to level off. Comparison of the regression lines were made for slope and elevation [Snedecor and Cochran, 1967]. The regression coefficients 6.65 for F+ and 6.98 for F− did not differ significantly (F = 3.12, df = 1,353, P > 0.05). There is a significant difference in the two lines with regard to elevation (F = 6.39, df = 1,354, P < 0.025). Young reared by lone females were significantly heavier than young reared by paired females. The young were 50% of the adult weight by the end of this study.

Behavior Events: Nursing Initiations, Social, Aggressive, and Maintenance Behaviors

Table 5 presents the observed nursing intiations for all subjects. Results of Mann-Whitney U-tests [Siegel, 1956] show that in both conditions, the young intitated significantly more times than did the females (U = 0 for both conditions; P < 0.003).
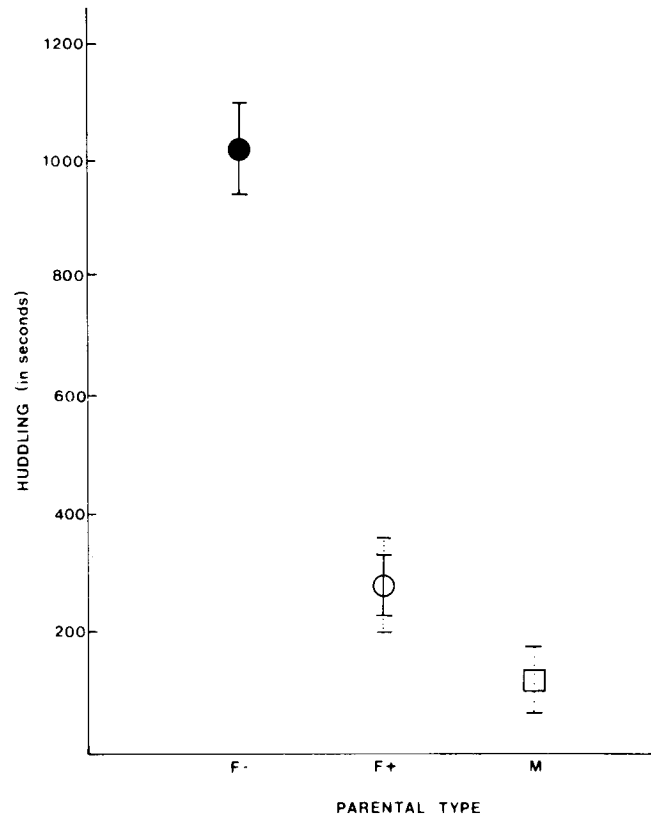
Fig. 2. Mean huddling of parental types per 30-min session over total observation time. Ninety-five percent least-significant confidence intervals (LSCIs) are placed about the mean values. Dotted lines represent LSCIs for F+ and M comparisons. Solid lines represent LSCIs for F+ and F− comparisons. Solid circle, F−; open circle, F+; open square, M.

Social and aggressive behaviors occurred erratically. Generally, either a behavior did not occur for a given day or it occurred frequently. Therefore, discrete behaviors were pooled into three categories (Table 2) for tabulation purposes. Absolute frequencies were not used; rather, the value used was the number of days any behavior in that category occurred. Wilcoxin matched-pairs signed-rank test was used for F+ and F− comparisons, and Mann-Whitney U-test was used for F+ and M comparisons [Siegel, 1956].

Social behavior was analyzed in two categories. All groups showed the same amount of exploratory sniffing (U = 10 for F+, M, P > 0.05; T = 5 for F+, F−, P > 0.05) and contact-promoting behavior (U = 5.5 for F+, M, P > 0.05; T = 7 for F+, F−, P > 0.05).
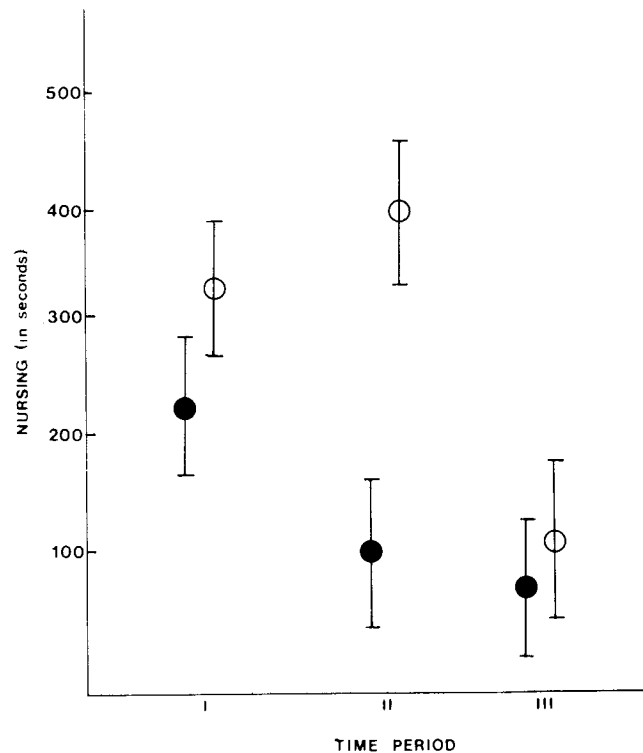
Fig. 3. Mean nursing of parental types by time interaction per 30-min session. Ninety-five percent Tukey's modified least-significant confidence intervals are placed about the mean values. Solid circles, F−; open circles, F+.

Aggressive behavior occurred at the same frequency for paired females and males (U = 11 for F+, M, P > 0.05). Yet lone females had significantly more aggressive encounters with the young than did paired females (T = 0 for F+, F−, P < 0.05).

Maintenance behavior data were tested with one-way analyses of variance. Because the methodology prescribed a maximum value of 120 for these behavior elements, analysis of the fifth behavior is dependent on the result of the first four. Therefore, only the following four behaviors were examined: rest, locomote, auto-groom, and forage.

The four maintenance behavior frequencies were totaled over the 24 observation days for each parental group. Daily means for each group were calculated by dividing the total by 120 (24 days × 5 subjects = 120). Percentages for daily means were found by dividing the daily mean by 120 (120 possible counts/day).

The vast majority of time was spent resting by all groups, although significant differences occurred among them. Males and paired females spent roughly 87–88%

of the observed day resting. Lone females rested significantly more than either males or paired females, for roughly 93% of the observed day.

Although locomoting and grooming comprised little of the *Kerodon's* observed day, differences were found among them. Lone females spent significantly less time engaging in both of these maintenance behaviors than the males or paired females. Males spent the most time moving in the cage (3.6%), and lone females spent the least amount of time (1.3%). Autogrooming was seen about 3% of the time in males and paired females and only about 2% of the time in lone females.

Animals were seen to feed both communally, at the food source, and solitarily, upon a wood perch or branch. Several instances of food stealing and food sharing by all members of the family were seen. Parents were observed to gnaw wood shelves and wire caging. No significant differences among parents were found in foraging behavior.

TABLE 4. Inventory of Litters by Female *Kerodon*

Female ID No.	Parturition date	Litter size	Litter sexes	Gestation (days)
7	5/13/78	1	M	—
	8/24/78	2	F, F	—
	11/7/78	1	F	75
	1/20/79	2	M, F	74
	4/5/79	1	F	75
	6/18/79	1	F[a]	74
	8/31/79	2	F[a], F[a]	74
8	8/30/78	2	M, M	—
	11/13/78	2	M, M	75
	1/28/79	2	M, F	76
	4/15/79	1	F	77
	6/30/79	2	M[a], F[a,b]	76
	9/12/79	2	M[a], M[a]	74
9	5/15/78	1	F	—
	8/20/78	2	M, F	—
	11/6/78	2	F, F	78
	1/20/79	3	M, F, F	75
	5/17/79	1	M[a]	—
	8/1/79	1	M[a]	78
10	1/12/79	2	M, F	—
	3/30/79	2	M, F	77
	6/15/79	1	M[a]	77
	8/31/79	1	F[a]	77
14	1/1/79	1	F	—
	7/20/79	2	M[a], M[a]	—
	10/6/79	1	F[a]	78
Mean		1.58± 0.73		75.9± 1.14

Means are presented ± 1 SE.
[a]Young used in study of maternal and paternal care.
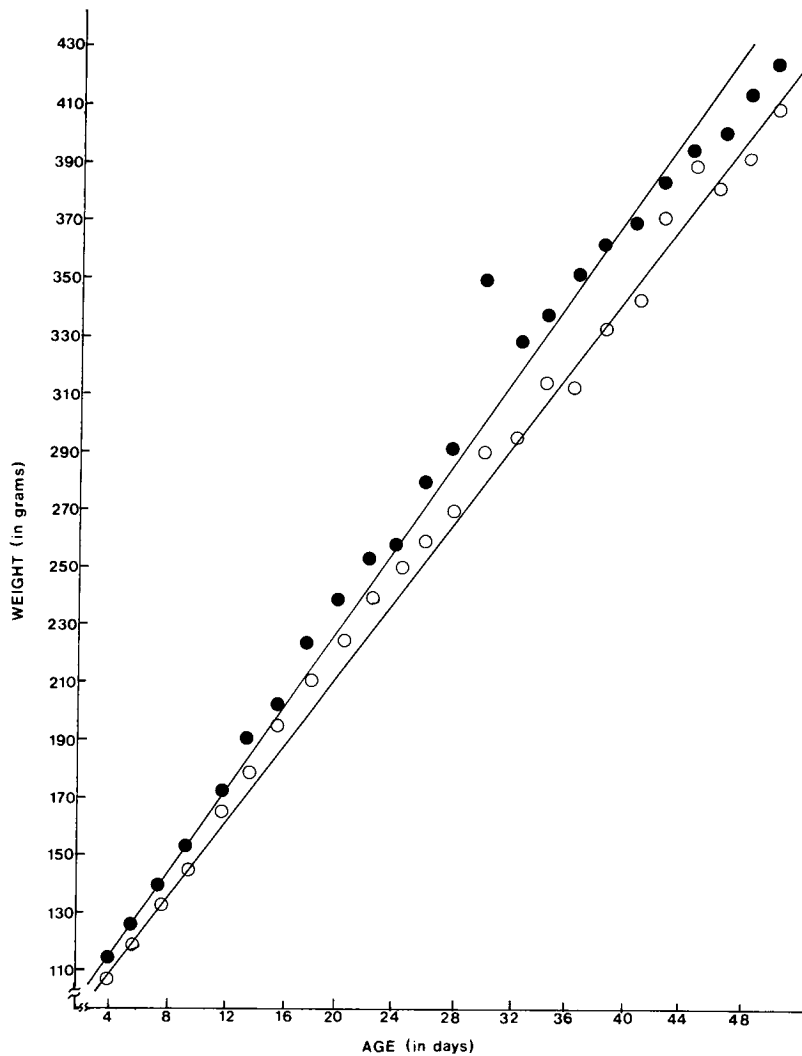[b]This female young died before completion of the study.

Fig. 4.   Mean weights for F− young and F+ young. The animals exhibit a relatively constant rate of growth. Equations for linear regressions are: $Y_{F-} = 96.2 + 6.98X$; $Y_{F+} = 88.1 + 6.65X$. Solid circles, F− young, open circles, F+ young.

Miscellaneous

Male courtship of the female was observed most often during the days following parturition. The male also courted the young as early as 1 day after birth. Two occurrences of an offspring mounting a female were observed; female 46 mounted female 7 on day 10, and male 41 mounted, with thrusting, female 14 on day 49.

No evidence of scent marking was observed among the *Kerodon* subjects studied.

Kerodon are precocial at birth. One newborn was seen to jump a height of 30 cm, climb 60 cm more, and then drop to the ground unscathed. At 4 days, it could jump vertically 1.2 m and land on all fours from a height of 1.5 m.

On three occassions, 4–5 sec perching by an offspring on a parent's back was observed for both males and females (Fig. 5).

During the present study, one death occurred without any apparent connection to the study. Female 40 was found dead at age 41 days. The cause was not clarified [NZP, 1979].

DISCUSSION

The results of this study will be discussed with reference to the behavior of *Kerodon* in captivity, and these discussions will be related to the social organization of *Kerodon* in the wild.

TABLE 5. Nursing Initiation Comparisons for All Female Subjects and Their Offspring

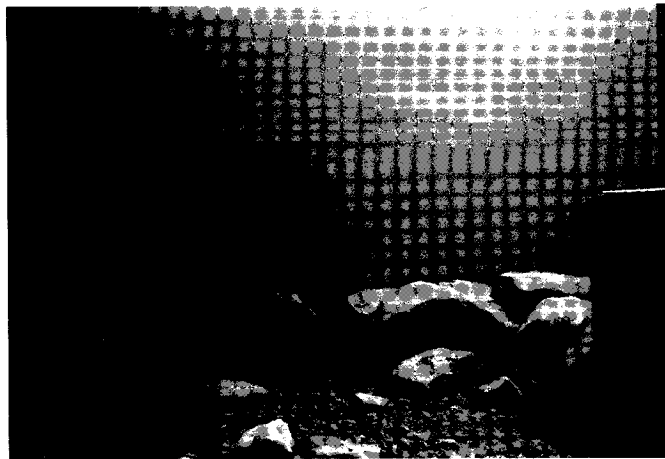| Female	Young initiate	Female initiate
7F+	27	0
8F+	53	0
9F+	19	4
10F+	27	1
14F+	50	0
7F−	45	5
8F−	10	0
9F−	29	0
10F−	26	3
14F−	14	0

Fig. 5.   Young perched upon father's back.

Female parents spent more total time with the young when the male was absent. Dudley [1974b] found this to be true of single parents and young regardless of the parent's sex in *P. californicus*. If the reduced frequency in contact time with young in paired females vs single mothers was due to mutual avoidance between the parents, one would expect F+ and F− differences to diminish when looking at huddles between one parent and the young. However, even when considering single parent huddling with young (type 1 huddle), the lone females spent more time with the young than did paired females. In addition, mutual avoidance in paired groups seems an unlikely explanation for the differences seen in total contact time, as agonistic behavior between mates was rarely observed. Possibly, the young attract the female more strongly when the other parent is absent. Alternatively, perhaps the lone female cannot escape from her offspring as easily as can the paired female.

The results indicate that, in total, lone females nursed less than paired females. This was most obvious in period II. Also, lone females were in contact with their offspring for a greater amount of time than paired females. The difference must be made up by more lone female-young huddles. This finding is similar to those of others who report that hystricomorph females housed with males during lactation huddle over the litter only while nursing, but solitary mothers often huddle when they are not nursing [Kleiman, 1974; Wilson, personal communication].

Both lone females and paired females exhibit reduced nursing behavior at the end of period II, which corresponds to Lacher's [1980] report of *Kerodon* weaning at 35.2 days. Throughout period III, both groups exhibited a trend of shorter nursing durations, in which no significant differences were found between the groups. It is thus concluded that, in this study, the absence of the male from the rearing environment does not alter the time of weaning.

Young reared by lone females were significantly heavier than young reared by paired females, although lone females did not nurse more than paired females. In fact, during period II, a significant increase in nursing behavior was seen in paired females. The weight discrepancy cannot be explained as an effect of litter size, since both groups were identically composed of three single litters and two twin litters.

The greater weight gain with less nursing in young raised by the mother alone is paradoxical. Rather than more nursing occurring in the paired female group, the females may have actually been producing less milk. The young then needed to suckle longer and more frequently to sustain adequate nourishment. Young reared by lone females may have received more than adequate quantities of milk and therefore gained more weight. Alternatively, young reared by two parents may have received more stimulation and less frequent rest, resulting in a greater energy expenditure. The study shows that the pairs tend to be more active than the single females. Perhaps their young are also more active.

The presence or absence of the father had no effect on frequency of mother-young nursing initiations. In both groups, female initiations occurred primarily in the first period, exhibiting a negative correlation with the number of days postpartum. Similar changes have been shown for *M. pratti* [Kleiman, 1972].

As noted above, male involvement with the young is dependent in part on the female's tolerance. *Kerodon* females are generally not aggressive, and so the opportunity for paternal care is heightened. In regard to pair-reared young, both males and females showed the same amount of limited aggressive behavior. An interesting result was that lone females showed a higher frequency of aggressive behavior toward the young than did paired females.

Prior to the present study, an attempt was made to house a trio of one male and two females, which failed after one of the females received severe bite wounds. Similar attempts by the National Zoological Park at forming breeding colonies of *Kerodon* have been made with much the same results. However, Lacher [personal communication] had no problem starting a *Kerodon* colony of four females and two males, after which new adults could no longer be introduced. Lacher suggests that the reproductive condition of the female may affect such attempts; a female near estrus may be very aggressive toward other females.

Although the amount of total contact time for the parental categories varied significantly, males, paired females, and lone females spent roughly 90% of their maintenance activities at rest. Other captive time-budget data for *Kerodon* are in agreement, showing 91–95% of the activity at rest [Lacher, 1980]. It is therefore concluded that the quantity of rest behavior is largely independent of group composition.

The results of this study suggest that the father does not actually contribute to his offspring's growth and nurturing, since the young gain more weight when he is absent. Yet fathers exert a strong social influence over their offspring as indicated by the great deal of time they spend huddling with the young.

In the same sense, the nursing-suckling interaction does not function only to provide nourishment. In *M. pratti,* suckling continued past the point of lactation [Kleiman, 1972]. This suggests that suckling serves more than just a nutritional purpose. It implies a socializing behavior of mother to offspring and offspring to mother [Kleiman, 1970]. Also, it has been regularly noted that many young hystrico-morph rodents are able to eat solid food much earlier than the time of weaning [Kleiman, 1974]. *Kerodon* in this study were observed eating vegetation 2 days after birth, yet they continued to suckle for 5 weeks. This suggests that the act of suckling endured past the young's nutritional need. Nonnutritive suckling could promote bonding between mother and young and contribute to the cohesion of the social group.

Although survival of the prereproductive individual is a key strategy in species preservation, it is not solely dependent upon physical parameters such as huddling for thermoregulation and suckling for nourishment. Aid-giving and aid-receiving behaviors in most species are based on a social bond [Brown, 1975] and work to preserve group cohesion within the social system. Thus, huddling and suckling are also socializing behaviors and need to be included as such when discussing survivorship of a species.

Lactational demands are energy costly to the female [Daly, 1980]. The paired females in this study nursed their young more than did lone females, yet these young gained less weight. Perhaps the male's presence inhibits or suppresses lactation sooner. This could aid the female by sparing her the excessive expenditure of energy. Instead, she would allow an energy-efficient behavior, nonnutritive suckling, to occur without loss of output. Thus, when the male is present, he may indirectly relieve the female of some of the parental care burden. This hypothesis needs further investigation.

Lacher [1980] reported no direct paternal care for *Kerodon* in the captive state. He has observed that breeding males completely ignore the offspring in their harem groups. If "direct paternal care" is defined as male behavior with immediate physical influence on the young which increases their survivorship—eg, grooming and hud-dling with the young [Kleiman and Malcolm, 1980]—then the present study does not support Lacher's findings. *Kerodon* males are found to be more than tolerant of their

young. As described above, they are commonly seen to huddle with their offspring. The analyses of social behavior, which includes grooming and sniffing, reveal that males participate as much as females. Furthermore, absence of the male does not change the amount of social behavior seen in the female.

I have, on one occasion, watched a male carry its offspring in its mouth for several seconds. A second male rested while its young sat perched on the males's back for 5 sec. Perching behavior is described for young *Cavia* during bouts of social grooming with the mother [Rood, 1972]. Observations such as these must be fully considered when attempting to describe the male *Kerodon's* parental role in the field.

Though captive studies need to be judged with caution [Kleiman and Malcolm, 1980], it is paradoxical that an apparently polygynous species in the wild cannot breed polygynously in captivity. *Kerodon* at NZP breed most successfully in pairs. Perhaps a reexamination of social organization of *Kerodon* utilizing the findings reported here might shed new light on the mating system and social structure.

CONCLUSIONS

Both male and female *Kerodon* exhibit parental care toward their young. While both parents show the same amount of contact-promoting behavior, the total contact time of a *Kerodon* parent with its young depends on the parent's sex and the rearing environment. Females spend more time than males with their offspring. Females raising young by themselves spend more time than paired females with their offspring. Young *Kerodon* raised by lone mothers gain more weight than young raised by both parents, yet they appear to nurse less overall. This paradox has no clear explanation. The absence of the father from the rearing environment does not alter the time of weaning.

Aggressive and social behaviors toward young (excluding nursing and huddling) occur erratically in *Kerodon* parents. Males and females show the same amount of social behavior toward their young, but lone females are more aggressive to their offspring than are paired females. The father does not contribute to his offsprings' growth, yet he exerts a strong social influence over them.

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