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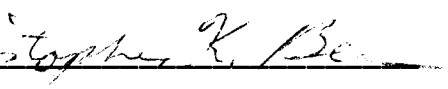
Signature 

Date 5/25/93

BEHAVIORAL DEVELOPMENT AND MATERNAL CARE IN CAPTIVE ERMINE (*MUSTELA ERMINEA*)

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Christopher Bern

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ABSTRACT

This thesis includes an ethological analysis of growth, behavioral development, and maternal care of a fast-growing mammal, the ermine. One litter of six ermine (*Mustela erminea*) was studied at the Minnesota Zoo. Observations began at around 30 days old and continued until around 80 days old. Duration and frequency of behaviors were recorded for each animal each day, concentrating on movement, non-movement, sleep, and play behaviors. Generally, activity increased with age, while inactivity remained the same or decreased. Additionally, there was an increase in duration and frequency of activity when the young were separated from the mother in week 12, and an unexplained increase in activity at week 10. Few differences were found between or within sexes for any behaviors before separation from the mother; after separation, ermine housed individually were more active than those housed together.

The behaviors of the mother were also noted. Maternal care was restricted to maintenance and protection, though this may be related to captive conditions. Changes in proximity to young over ontogeny were inconclusive.

Young and mother were mated with adult males when the young were 41 days old. The adult males mated readily with the young and they did not discriminate between sexes in mating

attempts. Adult males mated longest with the adult female and shortest with juvenile males.

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Chapter I

INTRODUCTION

Importance of Studying Juveniles

Behavioral development, growth, and parental care are factors that can fundamentally influence later reproduction and fitness. What happens to an animal during the juvenile period sets the pattern for adult characteristics as well as those of its offspring (Hofer, 1981; Bekoff, 1989). Understanding how these factors influence juveniles is crucial to understanding their effect on reproductive output.

The development of behavior influences reproduction in many ways. Young must learn skills necessary to survive to reproductive age and beyond. For example, herbivores and omnivores may learn how to forage safely (Asa, 1987), and carnivores are often taught how to hunt effectively (Liers, 1951; Kruuk and Turner, 1967; Ewer, 1973; Caro, 1979, 1980a, 1980b; Lode, 1989). In addition to feeding strategies, young must learn how to survive encounters with both conspecifics and potential prey. Young are required to learn when to escalate an interaction that could harm an opponent, how to assess a situation based on their own fighting ability, when to terminate an aggressive encounter, and generally learn how to communicate

aggression and submission (Bekoff, 1981; Bekoff and Byers, 1985). These skills can have a significant impact on reproductive success.

The growth of an animal also influences reproduction. The amount of nutrition young receive determine their growth rate and eventual size. In captivity, mammalian young that are provisioned reach adult size quicker and have a larger adult size than young who rely only on the mother (Ewer, 1973). Larger size can affect reproduction, as larger animals often win agnostic encounters, such as male-male competition for females (Clutton-Brock *et al.*, 1982). Increased size can also enable an animal to survive longer (being able to store more fat), and therefore have more reproductive opportunities. The rate of physical development is also important. Armitage (1981) found that in ground squirrels (*Cynomys* sp., *Marmota* sp., *Spermophilus* sp.), individuals who reached an adult size quicker and had their first reproduction delayed showed an increased level of social interaction.

Parental care, the third factor mentioned above, mainly influences the survival of the young. Among mammals, young are wholly dependent on the mother's milk, at least initially, and after weaning are often dependent on her to provide food until they learn how to forage for themselves (Ewer, 1973). The parents also protect the young from a potentially harmful environment, help keep them thermoregulated (Hofer, 1981), and in carnivores often teach the young necessary hunting skills (Kruuk and Turner, 1967; Ewer, 1973; Caro, 1980b; Lode, 1989). All of these events impinge on the young's

ability to survive to reproductive age. But parents can have other influences. For example, mothers have been shown to regulate hormonal state in young, as well as the onset of puberty (Hofer, 1981). Parental influence can indeed go beyond immediate offspring: in mice and rats, experiential effects are not only found with offspring but with grandpups as well (Hofer, 1981).

Because growth, behavioral development, and maternal care are critical to adult reproduction and fitness, it is important to understand what factors influence variation in these traits. This is the focus of the present study. The following is a brief introduction to what independent variables are known to be influential.

One of the primary factors influencing behavioral development is the habitat in which the young animal grows. Habitat differences can range from temperature to diet. Hull (1973) proposed the idea that animals in a warm environment grow faster, because they are able to divert energy from thermoregulation to growth. The general harshness of the environment, defined as the length of time food is readily available, is also influential. Marmots (*Marmota* sp.) in an environment with a longer growing season must have a greater percentage of adult body weight at dispersal than conspecifics in climates with a shorter growing season, requiring them to delay the age of dispersal and sexual maturity until the appropriate growth level is reached (Barash, 1974). Vervet monkeys (*Cercopithecus aethiops*) in a stressed habitat (defined as having periodic droughts) have an earlier weaning age than conspecifics in less stressed areas,

because the mother terminates investment when the risks become high. This has a detrimental effect on juveniles, as those who are prematurely weaned are less likely to survive or reach a healthy adult weight (Lee, 1984). Diet also plays a role in influencing development, as shown by Berger (1979) in bighorn sheep (*Ovis canadensis*) living in mountain and desert habitats. He found that desert-dwelling individuals were more precocial, grew faster, had earlier testicular descent, had earlier sexual maturity, played less, and had less behavioral diversity (i.e. a smaller behavioral repertoire) than conspecifics living in mountains. Individuals living in a desert habitat had less readily available food, forcing them to forage more, play less, and disperse earlier from the natal group.

Physical growth is also influenced by several factors. As would be expected, larger animals show a greater absolute g/day growth rate, but a slower relative growth rate. Diet is an important variable for explaining variations in growth rates across species. In the Carnivora, meat eating is associated with faster growth rates than herbivores or folivores. The type of parental care is also influential, with purely maternal systems leading to a slower rate of growth than biparental or communal systems (Gittleman and Oftedal, 1987).

The strategy that an animal adopts for parental care is related to ecology, mating system, and a combination of its diet, reproductive rate, body size, life span, and phylogeny (Klopfer, 1981; Gittleman and Oftedal, 1987; for review see Clutton-Brock, 1991). Hormones control maternal behavior from pregnancy to the dispersal of the

young (Rosenblatt and Siegel, 1981), as do the behavior of the young themselves (Harper, 1981). The issue of parental care will be dealt with in more detail in Chapter III.

It must also be recognized that growth, behavioral development, and maternal care are not independent. The growth rate of an organism is affected by its system of parental care (Gittleman and Oftedal, 1987). What happens during the behavioral ontogeny of an animal can affect how it behaves as a parent (Donaldson *et al.*, 1971; Nadler, 1974; Brunelli *et al.*, 1985). And the growth of an organism, specifically how long it takes to reach sexual maturity or adult size, can have an influence on its behavior (Barash, 1974; Massaro *et al.*, 1974; Kendrick, 1984; Ims, 1990). Therefore analyzing the interactive effects of these factors is essential to understanding variation in each factor, as will be examined in this thesis.

The Ermine

Carnivores are an especially interesting group to study because of their wide diversity of life history traits (Gittleman, 1986, 1993). Body size ranges from 365 kg in the polar bear (*Thalarctos maritimus*) to .08 kg in the least weasel (*Mustela rixosa*) (Gittleman, 1986). Variation in growth rate mirrors this pattern, from 1.5 g/day

in the least weasel to 122.2 g/day in the African lion (*Panthera leo*) (Gittleman and Oftedal, 1987). There is also a vast range of diets among the carnivores, ranging from the herbivorous giant panda (*Ailuropoda melanoleuca*) to omnivorous procyonids and canids, to strictly carnivorous mustelids and felids (Ewer, 1973; Gittleman, 1986). Carnivores inhabit virtually every habitat, from arctic tundra to tropical rain forests, and even the sea, showing a diversity of habitat associations that no other mammalian order has matched. These traits combine to make the carnivores a most diverse and interesting mammalian group to examine variation in growth, behavioral development, and parental care.

Even with this great diversity, several patterns emerge within the order. Female body weight is positively correlated with birth weight and with both individual and litter growth rates (Gittleman, 1986; Gittleman and Oftedal, 1987). In fact, virtually all absolute life history variables are positively correlated. "Gestation length, birth weight, weaning age, age of independence, age of sexual maturity, longevity, inter-birth interval, and litter weight are all positively correlated; litter size is negatively correlated with gestation length, age of independence, and age of sexual maturity" (Gittleman, 1986: 755). All in all, there is a close relationship between adult body size or brain size and life histories (Gittleman, 1986).

Though most life histories in carnivores follow predictable trends, certain species interestingly stand out. The ermine (*Mustela erminea*, also called the stoat or short-tailed weasel) is a prime

example. Ermine have particularly rapid development, almost the fastest among carnivores. The total growth of the litter is unusually rapid compared to the female's body weight (Gittleman and Oftedal, 1987). This rapid growth rate is especially striking in the light of ermine being asocial, with exclusively maternal care (King, 1989), where the entire energetic demand of a litter is placed with a female. As mentioned above, carnivores with maternal care systems should have the slowest growth rates when compared to carnivores with biparental or communal care of juveniles (Gittleman and Oftedal, 1987), yet the ermine has one of the fastest.

Ermine exhibit several other unusual characteristics. Basal metabolic rate and level of activity are extremely high. For their weight, ermine are arguably the most aggressive and fearless carnivore, often bringing down prey many times their size, and even behaving aggressively towards humans (King, 1989). Ermine also have delayed implantation, which though not unusual among carnivores (Ewer, 1973; Gittleman, 1986), may contribute to the phenomenon of neonatal breeding, wherein an adult male will mate with neonatal females when he is in the burrow to mate with the adult female. It is thought that those neonates will subsequently give birth to a healthy litter the following season (DonCarlos *et al.* 1986; King, 1989). This unusual phenomenon of neonatal breeding underscores the need to better understand growth, behavioral development, and maternal care in weasels.

Even though the ermine possess such extreme trends they have been little studied. Studies to date have considered the behavior of neonatal and juvenile weasels in passing or in little detail, concentrating primarily on physical growth and development. Hartman (1964) deals almost exclusively with reproduction and physical development, with some additional data on vocalizations. East and Lockie (1965) devoted only one paragraph on the play and killing behavior of juvenile ermine, concentrating instead on the timing of mating and the ontogeny of physical characteristics during the first two months of life. Heidt *et al.* (1968: 417) state of *M. nivalis* that "by the 40th day the young...were observed in aggressive and reproductive play behavior," yet the authors never define or further describe these behaviors, making this observation ambiguous. They also concentrate on physical development, while only mentioning that it appeared that the mother "taught" the young to kill by killing mice while young dangled from her neck region (the young "learned" how to kill by being present when a kill was made). Heidt (1970) continued this work, focusing on killing and threat behavior, and growth and physical development. His summary of observational methods best sums up previous methods and behavioral studies of weasels: "Behavior patterns were observed at irregular intervals throughout the maturation of the young animals" (Heidt, 1970: 233).

This thesis therefore considers previously unstudied or poorly described aspects of the behavioral development of ermine.

Physiological development will be downplayed, as previous studies have concentrated in this area. Contents are divided into three parts, considering different aspects of and influences on the early life of ermine. The first will examine play, sleeping, movement, and "non-movement" in juveniles. The second will look at maternal care and interactions with the young. The final section will describe neonatal breeding, specifically breeding trials with three adult males.

Chapter II

DEVELOPMENT OF YOUNG

Introduction

Several studies have examined growth and behavioral development of species within the genus *Mustela*. However, as mentioned in Chapter I, these studies do not describe the full range of behaviors, as in an ethogram, and how they change during early development. Hartman (1964), East and Lockie (1965), Heidt *et al.* (1968), and Heidt (1970) all focused on the timing of reproduction, parturition, and ensuing physical growth and development of the young. Poole (1966, 1978) provided detailed descriptions of play and aggression in the polecat (*Mustela putorius*), yet data were not gathered on ontogeny. Two studies have considered sex differences in the play of juvenile ferrets (*M. putorius furo*), showing that males perform more neckbiting and "stand-over" behaviors but the sexes are similar in other play behaviors (Biben, 1982; Stockman *et al.*, 1986). Yet, again the changes in patterns were not studied.

The lack of available information on the ontogeny of behavior is especially surprising considering the ease in managing and rearing ermine and other *Mustela* species in captivity. Ermine may be housed in relatively small enclosures while remaining healthy and active. Individual animals breed readily in captivity and the young

are usually hearty and easy to manage (DonCarlos, personal communication; Feder, personal communication). Therefore studies of juvenile behavioral development are relatively accessible, particularly in comparison to most other carnivores (Ewer, 1973; Gittleman, 1989). Such studies would be useful in understanding the ontogeny of behavior in solitary carnivores, ranging through all of the mustelids and possibly across other families of Carnivora (see Bekoff, 1989).

This chapter will therefore examine the behavioral repertoire of juvenile ermine, concentrating on how these behaviors change during ontogeny. Particular basic behaviors such as movement, non-movement, play, and sleep (all defined below) will be described in detail. Physical characteristics will be downplayed, as these have been previously studied.

Methods

Subjects

The study animals consisted of one litter of six individuals (four males and two females), born on April 10, 1992. The mother was captured in the wild and housed at the Minnesota Zoo beginning in April 1991. She was estimated to be one year old at the time of

capture. The study litter resulted from a captive mating with a captive-bred male.

Subjects were shaved on various parts of the head and body with electric clippers to allow quick individual recognition. Subjects were also assigned numbers and letters (Males: 1M, 2M, 3M, 4M; Females: 1F, 2F).

Housing

The study was performed at the Minnesota Zoo in Apple Valley, Minnesota. The study animals were housed in an alcove in the back of a small aviary, out of public view and access. Birds rarely flew into the area of the cage, and a clear plexiglass sheet was placed on the top of the cage to prevent encounters with the birds. Birds were all small, mostly songbirds native to Minnesota, which these animals could have encountered in the wild.

Animals were housed in a large whelping cage, used previously by the zoo for the breeding of ermine. The cage was made of plywood with a wire mesh front and top. Two plexiglass nestboxes were attached at opposite sides (Figure 2-1). The nestboxes were clear on the top and two sides. The remaining sides were opaque and the clear sides were covered with black cloth flaps when observations were not being carried out. This design allowed ease in direct observations in nestboxes, while darkening the nest most of

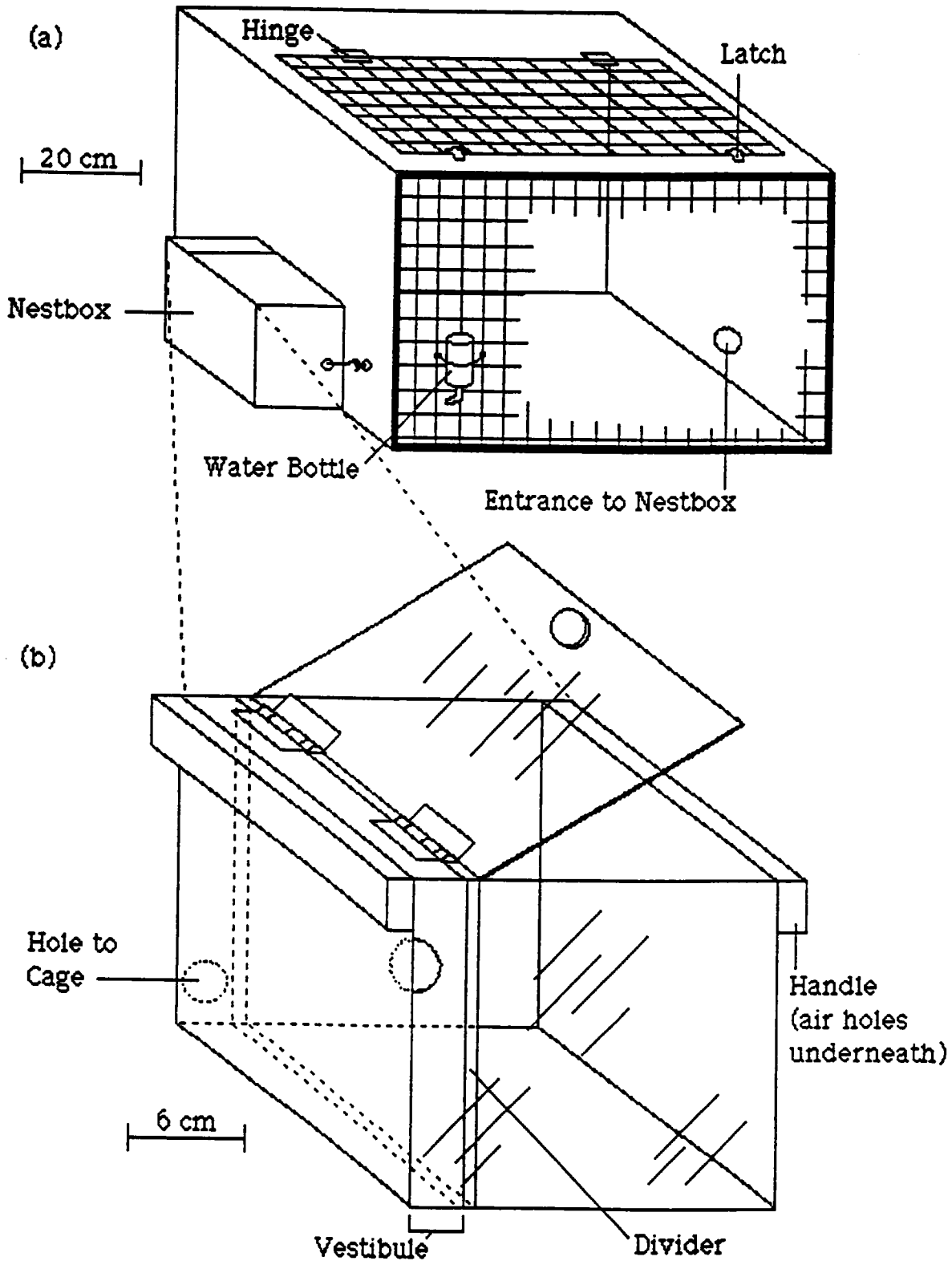

Figure 2-1. Diagram of (a) cage and (b) nestbox. Front, right side, and top of nestbbox are clear plexiglass; other sides are opaque.

the time, giving the ermine a semblance of being in a burrow. During observations the ermine were allowed to habituate, after the flaps were raised, before any observations were made. The nestbox contained a removable divider with a single opening near the roof of the nestbox to prevent the young from easily leaving the nest while their movements were still unsteady, yet allowing the mother easy access to and from the nestbox. This divider was removed at 39 days.

Wood shavings were provided in the cage and nestboxes. Water was provided *ad libitum.* Thawed frozen adult mice were used as food. Keepers checked the cage twice each day, once in the morning and again in the evening. If the cage was empty of mice, they would provide new ones, increasing the amount as the juveniles aged, until 6-8 mice were provided daily for the litter and adult female. Only mostly eaten mice were removed and replaced; half-eaten mice were left in the cage until completely consumed to maximize usage of food (DonCarlos, personal communication).

At 49 days, a branch and a small hollow log were placed in the cage as climbing and play items. At 75 days, two small transfer boxes (see DonCarlos *et al.*, 1986 for a description) were placed in the cage to acclimate the animals in preparation for separation from the mother.

The juveniles were separated from their mother at 80 days. Three juveniles (1M, 2M, and 1F) were kept together while the other three were housed separately and treated as adults (for adult

management procedures see DonCarlos *et al.*, 1986). These individuals were chosen essentially randomly, being numerically first within each sex. They were separated in order to see if there were any differences based on social conditions after separation, as well as to maximize the exhibit's appeal to the public. Once separated, all subjects were placed on public exhibit on a rotating schedule.

Juveniles were weighed weekly, minimizing direct contact and handling time so as to not disturb the animals. During these weighings, the shaved markings were changed or reinforced.

Observational Methods

Observations began on May 13, 1992 and continued until July 22. The litter was born earlier than expected, and scheduling conflicts prevented observations before the young were 33 days old. Focal animal sampling (Altmann, 1974) of juveniles was made for 10 min. periods per animal each day. The order in which individuals were observed each day was randomized. Subjects were observed at different times each day on a rotating schedule, from 800-2000 hours. After the juveniles were separated, all available adults were also observed, using the same methods as for the juveniles. These adult observations were combined to form a stereotypical adult database to compare to the juveniles.

Observations were made on a Hewlett Packard 71B hand-held data recorder using Timeit, a data-collecting program which records frequency and duration behaviors in real-time. Computer recorded data were supplemented by notations on a checksheet, keeping a general record of activities and location of non-focal animals in 1 min. intervals. General comments on behaviors and data collection were made in a notebook at the end of each day. Table A-1 lists the behaviors observed and the definitions for each. For behaviors involving two or more individuals (associations, play, etc.) an attempt was made to note who initiated the behavior, though this was not always possible to determine.

Data were analyzed to assess weekly and daily (in 2 hr. samples) trends. A t-test was used to test for differences between individuals and between categories. An ANOVA (α=0.05) was performed on the Mean Bout Length per week for movement, non-movement, play, and sleep in juveniles. A Fisher's PLSD (Protected Least Significant Difference), a multiple t-test of all possible pairwise comparisons, was performed for each of the above four behaviors to note specific differences between weeks. To account for possible heterogeneity of variation in the data, a Scheffe's F test was also run, and though values are not given, agreed with all results of the Fisher's PLSD.

Results

Physical Growth and Development

Body weight increased rapidly throughout the developmental period, beginning to level off at about week 7 for females and week 12 for males. Males and females were of approximately equal weight until week 4 (Figure 2-2). Among individuals, 4M was the heaviest male and 2F the heaviest female, with these relative weights within sexes remaining stable. The litter as a whole showed the most rapid growth between weeks 4 and 8 (Figure 2-3). After separation from the mother, the juveniles kept together decreased in weight, while those housed individually either maintained a relatively constant weight, or, in the case of 3M, increased weight. Body length generally increased along the same pattern as weight (Figure 2-4), though precise measurements were not taken.

Eyes began opening at 38 days. At that time 2F had both open, with 2M and 3M beginning to open. At 39 days 1M, 2M, and 3M had all opened fully. At 40 days 1F had both open fully and 4M's were both half-open. By 41 days all subjects' eyes were fully opened.

Locomotion/Movement

At the beginning of the study at 33 days of age, the young were mobile though unsteady. Fore- and hind-limbs were uncoordinated and did not move synchronously. When young

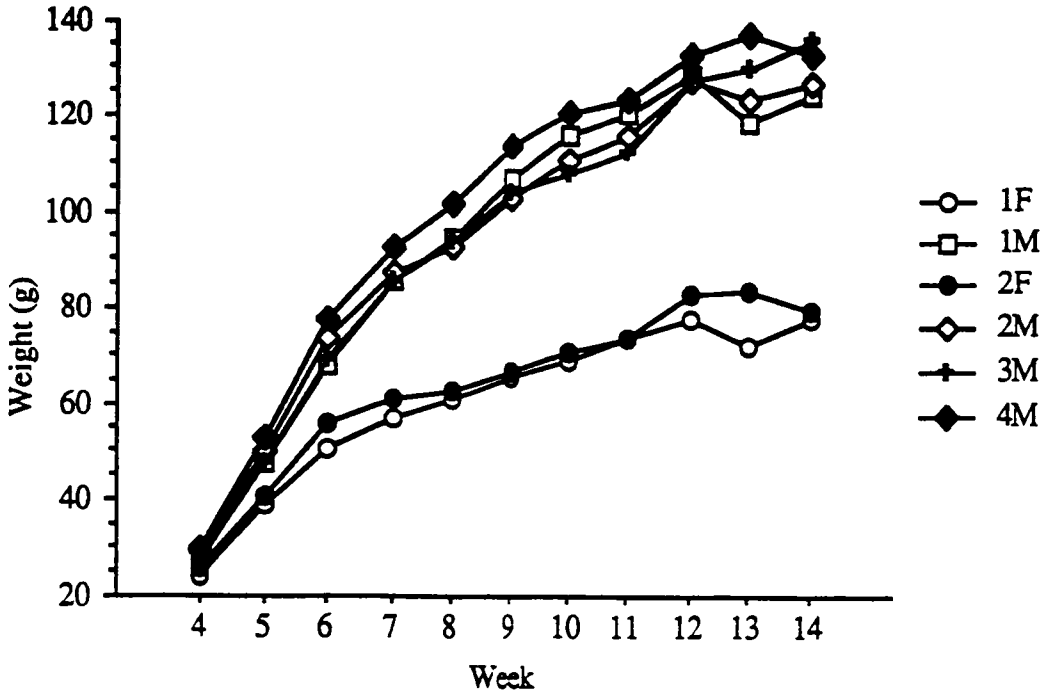

Figure 2-2. Weight of individual juveniles, per week.

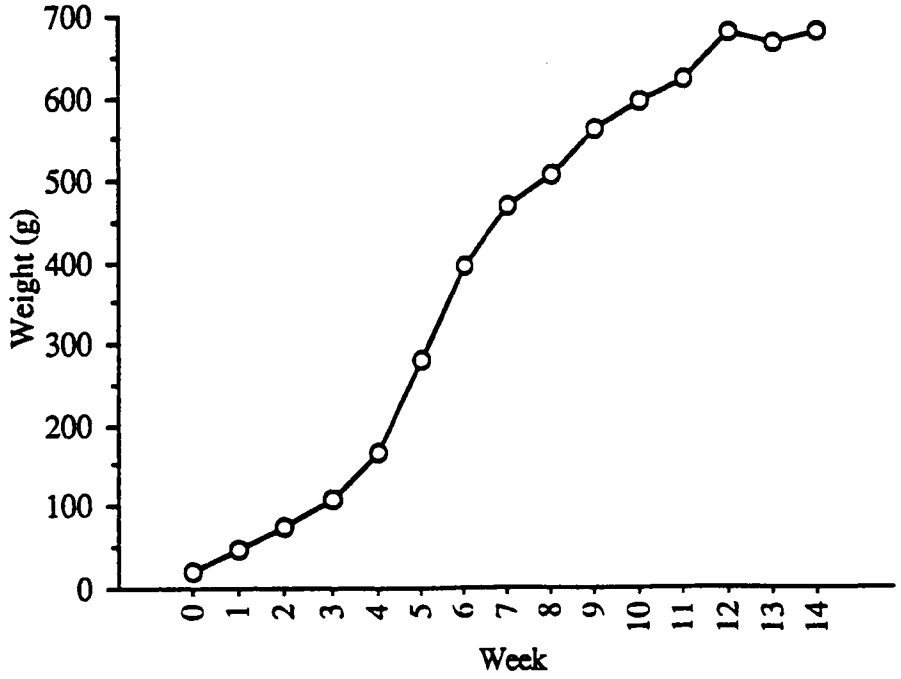

Figure 2-3. Weight of litter per week.

(a)



(b)



Figure 2-4. Physical development of 2M at (a) 38 days old and (b) 45 days old.

attempted to stand and move the body was shaky, wobbling laterally. At this age they were able to leave the nestbox into the vestibule with much effort and difficulty. An ermine would raise the body and throw the front limbs onto the lip of the hole, then push with the hind limbs, trying to squirm through the entrance. Most attempts failed. When a juvenile managed to make it into the vestibule area, it was usually quickly taken back into the nestbox by the mother.

By 39 days (when the dividers were removed from the nestboxes) the young were leaving the nestbox and moving around the cage, though they still spent most of the time in the nestboxes. They were still unsteady, with lateral wobbling, though they were able to make quick dashes across the cage. Most of the support came from the front limbs, the hind limbs almost dragging behind.

At 41 days increased steadiness could be seen, though the hind limbs did not seem as steady as their front. At 42 days playing began, showing an increased degree of coordination. Movement across the cage was in the alternating-limb movement and hopping gait of an adult. At 43 days the hind limbs were still weak, with the pelvis twisting around the spinal joints. Differences in developmental changes among littermates were not detected.

Development continued rapidly. By 47 days there was almost no instability in the hind limbs. By 49 days the young were spending more time in the cage and were able to climb on the wire

front. By 53 days there was no unsteadiness in locomotion and fully adult movement was observed.

Juveniles spent most of their time in the nestboxes until week 10, when time in the nestboxes dropped sharply (Figure 2-5). Conversely, the duration and total amount of time spent in the cage area (Figures 2-6 and 2-7, respectively) increased each week beginning at week 7.

Over the entire study period movement bouts lasted a mean of 48.551 s (n=1063, s.d.=71.691). The mean bout length (hereafter referred to as MBL) showed little variation as the young aged (Figure 2-8), though it tended to increase. An increase in MBL occurred in week 12, likely coinciding with separation from each other and from the mother.

There is a significant difference in MBL among weeks ($F=6.399$; $d.f.=10, 1052$; $p<0.0001$). Looking at differences between weeks (Table 2-1), several groups emerge that are similar to each other, but different than other weeks: 4, 5-11, and 12-14.

Movement also tended to decrease with time of day, being greatest in the morning (Figure 2-9). Though there were no significant changes between weeks during most of ontogeny (specifically up to week 11), the overall time spent moving did increase (Figure 2-10), especially after the young were separated. Besides this increase, weeks 5-7 are approximately the same. Week 10 stands out because of the sudden increase in the amount of movement followed by a decrease.

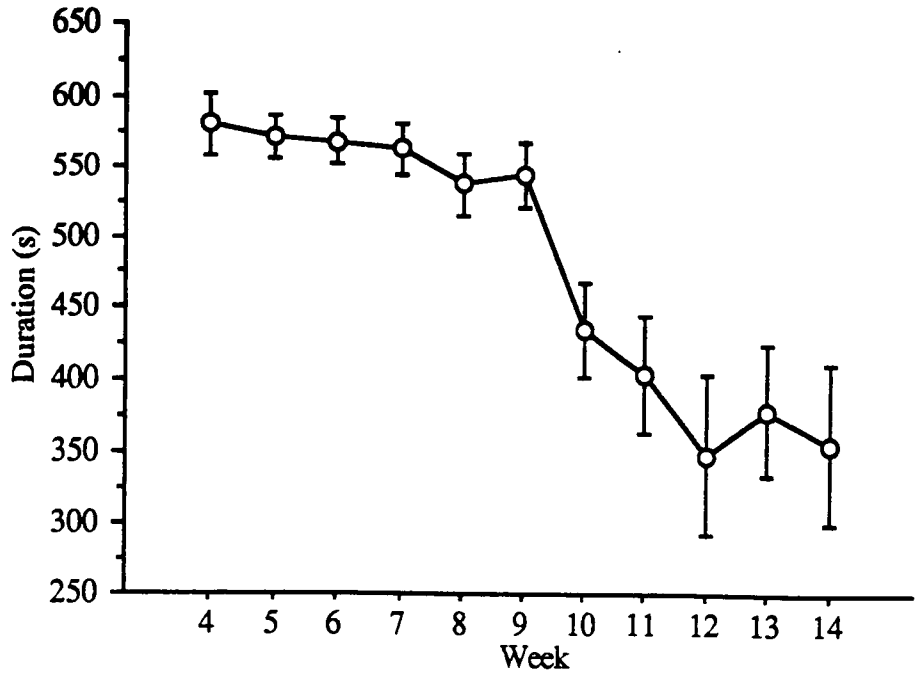

Figure 2-5. MBL +/- S.E. of remaining in a nestbox per week.

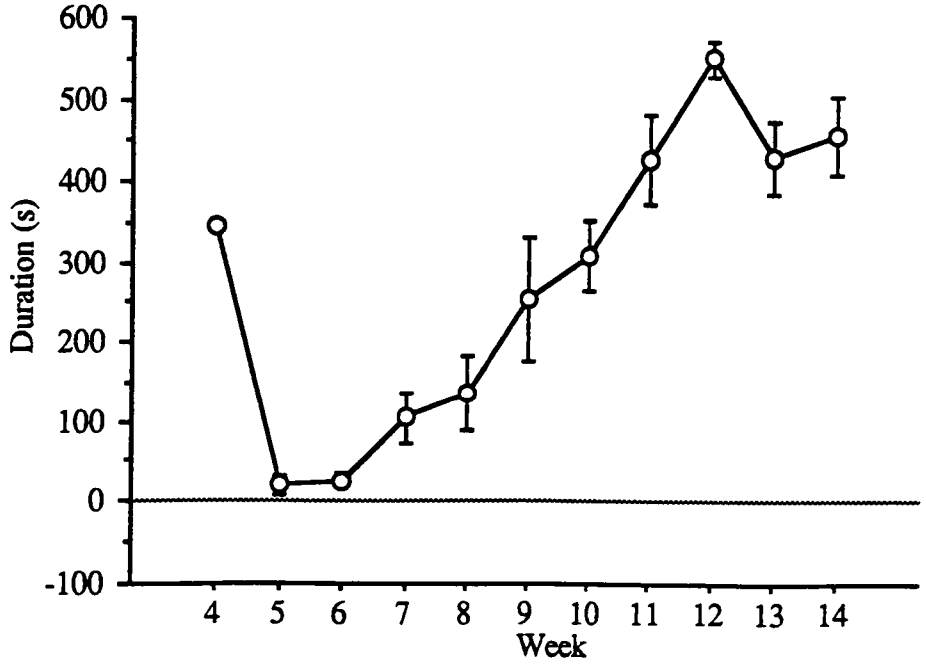

Figure 2-6. MBL +/- S.E. of being in the cage per week.

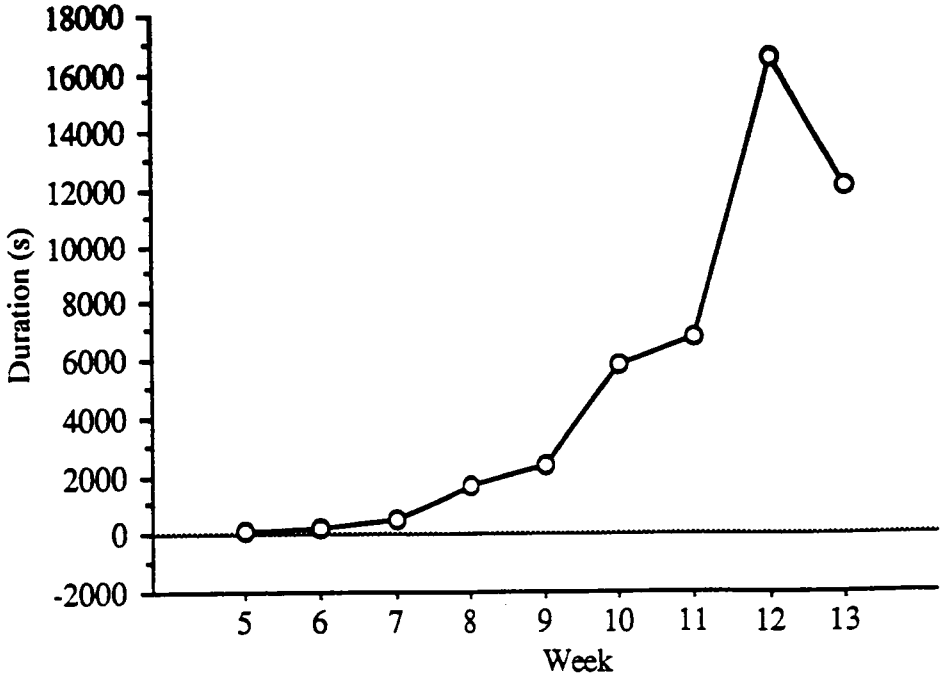

Figure 2-7. Total amount of time spent in the cage per week.

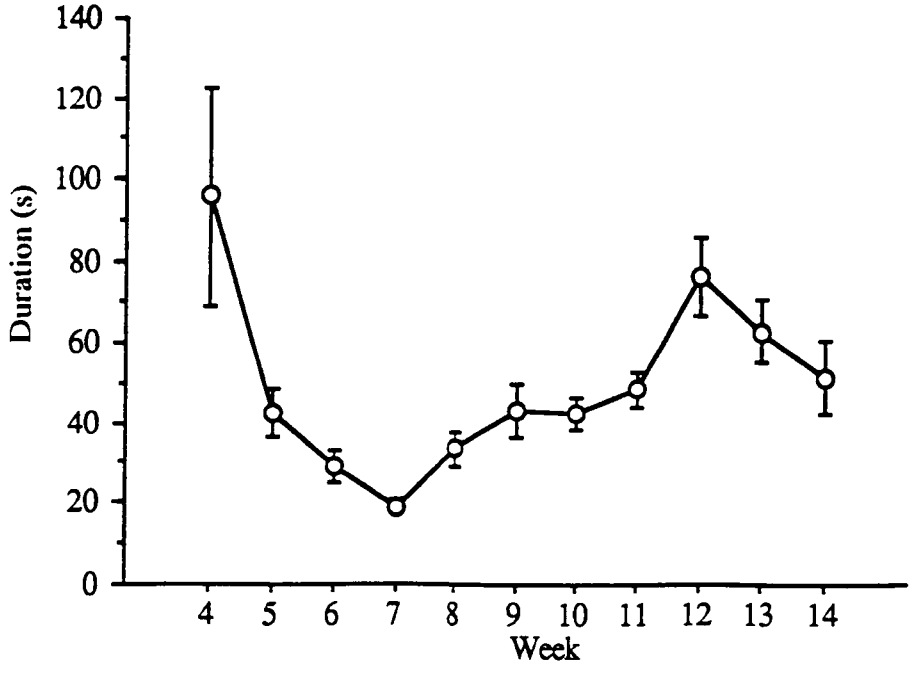

Figure 2-8. MBL +/- S.E. for movement per week.

Table 2-1. Results of Fisher's PLSD between weeks for MBL of movement.

Weeks	p	Weeks	p
4, 5	0.01	7, 8	n.s.
4, 6	0.0001	7, 9	0.05
4, 7	0.0001	7, 10	0.05
4, 8	0.001	7, 11	0.01
4, 9	0.01	7, 12	0.0001
4, 10	0.001	7, 13	0.0001
4, 11	0.01	7, 14	0.01
4, 12	n.s.	8, 9	n.s.
4, 13	0.05	8, 10	n.s.
4, 14	0.01	8, 11	n.s.
5, 6	n.s.	8, 12	0.0001
5, 7	0.05	8, 13	0.01
5, 8	n.s.	8, 14	n.s.
5, 9	n.s.	9, 10	n.s.
5, 10	n.s.	9, 11	n.s.
5, 11	n.s.	9, 12	0.01
5, 12	0.001	9, 13	0.05
5, 13	0.05	9, 14	n.s.
5, 14	n.s.	10, 11	n.s.
6, 7	n.s.	10, 12	0.0001
6, 8	n.s.	10, 13	0.05
6, 9	n.s.	10, 14	n.s.
6, 10	n.s.	11, 12	0.01
6, 11	n.s.	11, 13	n.s.
6, 12	0.0001	11, 14	n.s.
6, 13	0.001	12, 13	n.s.
6, 14	0.05	12, 14	0.01
		13, 14	n.s.

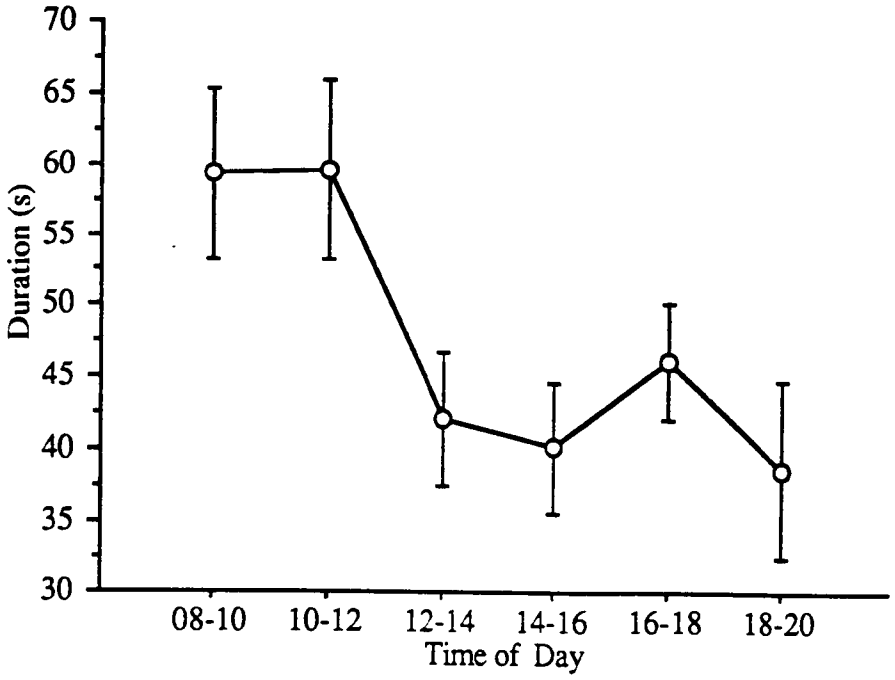

Figure 2-9. MBL +/- S.E. for movement per time of day.



Figure 2-10. Total amount of time spent moving per week.

Before the young were separated, there were no significant differences in MBL of movement between sexes or between females. Male 3 did have a significantly lower MBL than 1M and 4M, though there were no other differences among males. After separation, females were significantly higher than males, with no differences between the two females. Neither male nor female young differed significantly from adults. Among males only 4M was different, showing significantly longer MBL's than all other males (Table 2-2).

As expected, since total time moving increased with weeks, total amount of time spent non-moving decreased (Figure 2-11). The MBL (overall 67.123 s, n=1115, s.d.=83.117) also decreased with time (Figure 2-12), though there was a slight increase after separation.

There is a significant difference in MBL among weeks ($F=10.302$; d.f.=10, 1104; $p<0.0001$). Looking at differences between weeks (Table 2-3), several groups emerge that are similar to each other, but different than other weeks: 4, 5-9, and 10-14. This pattern parallels that observed for movement.

Over the day, females peaked during the 10-12 and 18-20 intervals and males peaked at the 12-14 interval (Figure 2-13). This difference in activity patterns between sexes was not observed in any of the other behaviors.

Before separation, no significant differences were found between or among males and females. After separation, there were still no differences between sexes or between adults and juveniles. However 1F had a significantly higher MBL than did 2F, and 2M and

Table 2-2. T-test values between categories for MBL of movement.

Individuals	Mean Diff.	DF	t-value	p
(a). Before separation from the mother.				
F, M	4.777	622	1.112	n.s.
1F, 2F	3.916	216	0.547	n.s.
1M, 2M	5.490	202	0.695	n.s.
1M, 3M	17.221	178	2.736	0.01
1M, 4M	2.397	170	0.289	n.s.
2M, 3M	11.731	204	1.681	n.s.
2M, 4M	-3.093	196	-0.362	n.s.
3M, 4M	-14.823	172	-2.092	0.05
(b). After separation from the mother.				
A, F	-2.117	142	-0.083	n.s.
A, M	18.691	343	1.034	n.s.
A, J	13.051	462	0.673	n.s.
F, M	20.808	437	2.126	0.05
1F, 2F	-12.447	117	-0.556	n.s.
1M, 2M	15.301	178	1.618	n.s.
1M, 3M	-2.492	161	-0.225	n.s.
1M, 4M	-46.382	153	-3.073	0.01
2M, 3M	-17.793	163	-1.755	n.s.
2M, 4M	-61.683	155	-4.325	0.0001
3M, 4M	-43.890	138	-2.683	0.01

A=all adults, F=all females, J=all juveniles, M=all males, Mean Diff.= mean difference between individuals in s., DF=degrees of freedom.

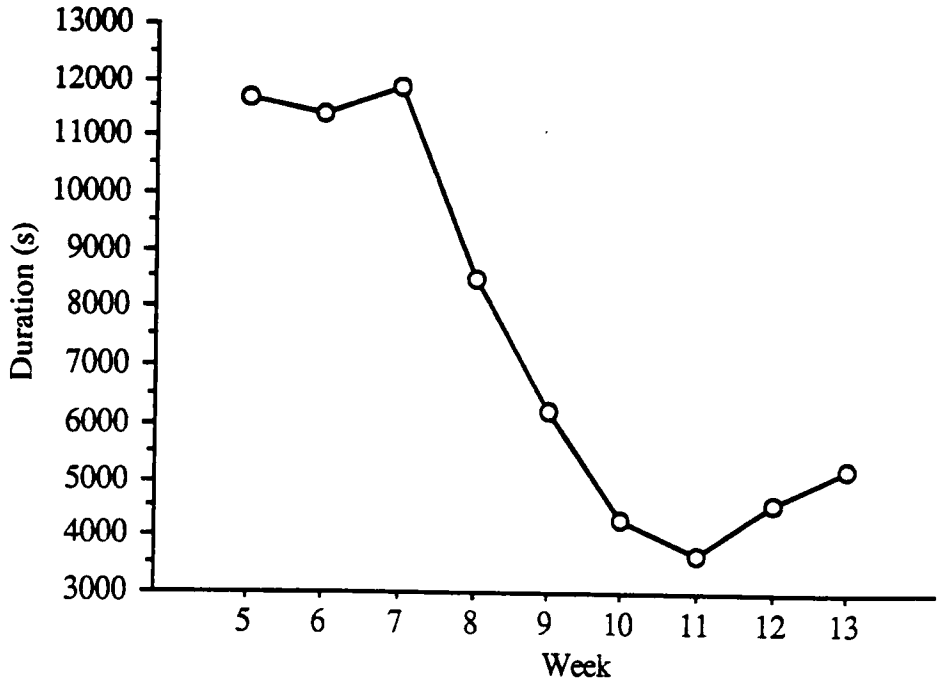

Figure 2-11. Total amount of time spent non-moving per week.

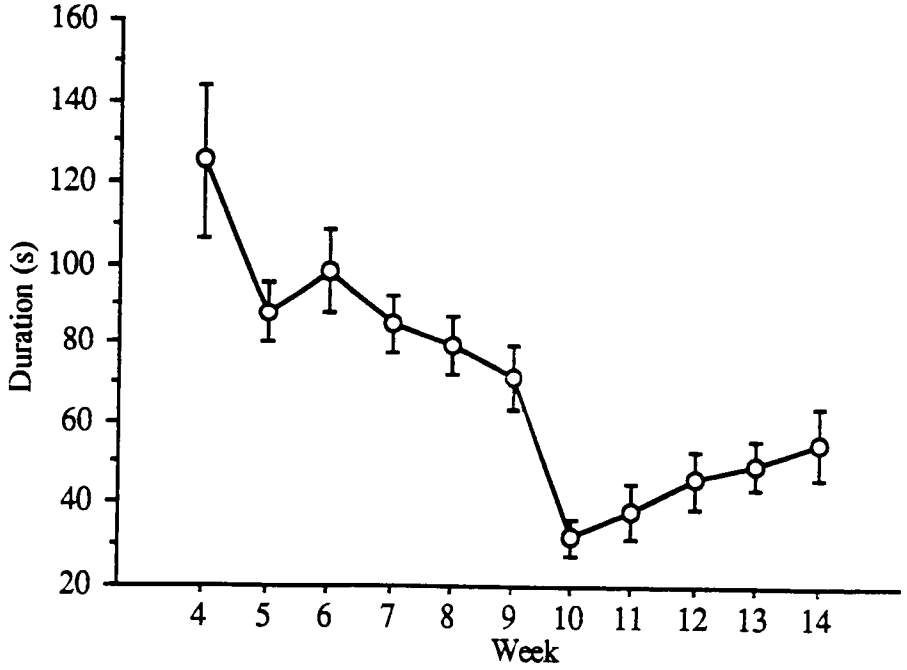

Figure 2-12. MBL +/- S.E. for non-movement per week.

Table 2-3. Results of Fisher's PLSD between weeks for MBL of non-movement.

Weeks	p	Weeks	p
4, 5	0.05	7, 8	n.s.
4, 6	n.s.	7, 9	n.s.
4, 7	0.05	7, 10	0.0001
4, 8	0.01	7, 11	0.0001
4, 9	0.01	7, 12	0.001
4, 10	0.0001	7, 13	0.001
4, 11	0.0001	7, 14	0.05
4, 12	0.0001	8, 9	n.s.
4, 13	0.0001	8, 10	0.0001
4, 14	0.0001	8, 11	0.001
5, 6	n.s.	8, 12	0.01
5, 7	n.s.	8, 13	0.01
5, 8	n.s.	8, 14	n.s.
5, 9	n.s.	9, 10	0.001
5, 10	0.0001	9, 11	0.01
5, 11	0.0001	9, 12	0.05
5, 12	0.0001	9, 13	n.s.
5, 13	0.001	9, 14	n.s.
5, 14	0.01	10, 11	n.s.
6, 7	n.s.	10, 12	n.s.
6, 8	n.s.	10, 13	n.s.
6, 9	0.0001	10, 14	0.05
6, 10	0.0001	11, 12	n.s.
6, 11	0.0001	11, 13	n.s.
6, 12	0.0001	11, 14	n.s.
6, 13	0.0001	12, 13	n.s.
6, 14	0.001	12, 14	n.s.
		13, 14	n.s.

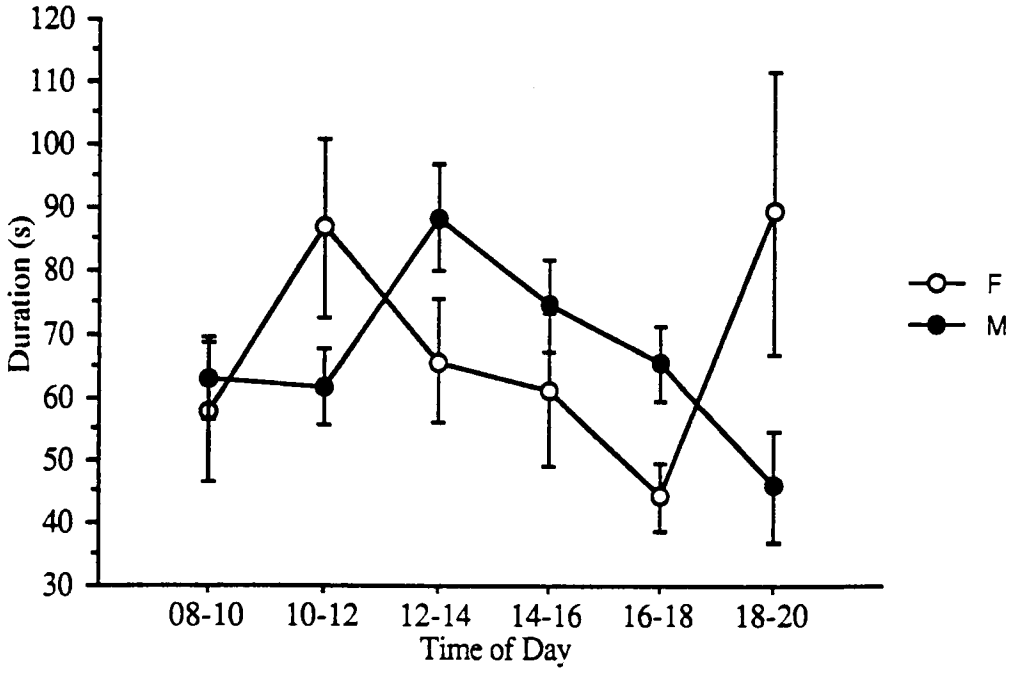

Figure 2-13. MBL +/- S.E. for non-movement per time of day.

3M were significantly higher than 4M. No other intra-sex differences were found (Table 2-4).

Sleeping

Juveniles slept for a mean of 4 min. and 17.006 s (n=430, s.d.=205.672). MBL increased until week 11, then began decreasing slightly (Figure 2-14). There is a significant difference in MBL among weeks ($F=7.431$; d.f.=10, 419; $p<0.0001$). Looking at differences between weeks (Table 2-5), several groups emerge that are similar to each other, but different than other weeks: 4-7, 8-9 and 13-14, and 10-12. Over the day, the lowest MBL occurred between 12-14, then increased as the day went on (Figure 2-15). The highest MBL occurred in the early morning and late evening, close to when the lights were out, though no strong correlation between photoperiod and sleep duration could be analyzed. The total amount of time spent sleeping peaked in weeks 8 and 9 and is lower in most other weeks (Figure 2-16).

Before separation there were no differences among females or males, except for 2M's MBL being greater than 4M. There was, however, a difference between sexes, females sleeping significantly longer than males. After separation there were no differences between sexes or between juveniles and adults. Among sexes, 1F was significantly greater than 2F, and 4M significantly less than 2M and 3M (Table 2-6).

Table 2-4. T-test values between categories for MBL of non-movement.

Individuals	Mean Diff.	DF	t-value	p
(a). Before separation from the mother.				
F, M	-11.661	780	-1.735	n.s.
1F, 2F	15.924	244	1.353	n.s.
1M, 2M	1.393	270	0.136	n.s.
1M, 3M	-17.106	281	-1.704	n.s.
1M, 4M	-12.188	273	-1.314	n.s.
2M, 3M	-18.499	259	-1.574	n.s.
2M, 4M	-13.581	251	-1.230	n.s.
3M, 4M	4.918	262	0.455	n.s.
(b). After separation from the mother.				
A, F	12.016	114	0.902	n.s.
A, M	9.744	277	0.709	n.s.
A, J	10.324	362	0.795	n.s.
F, M	-2.272	331	-0.263	n.s.
1F, 2F	31.431	83	2.334	0.05
1M, 2M	-14.399	114	-1.095	n.s.
1M, 3M	-23.784	143	-1.809	n.s.
1M, 4M	19.977	119	1.821	n.s.
2M, 3M	-9.385	125	-0.653	n.s.
2M, 4M	34.376	101	3.125	0.01
3M, 4M	43.761	130	3.505	0.001

A=all adults, F=all females, J=all juveniles, M=all males, Mean Diff.= mean difference between individuals in s., DF=degrees of freedom.

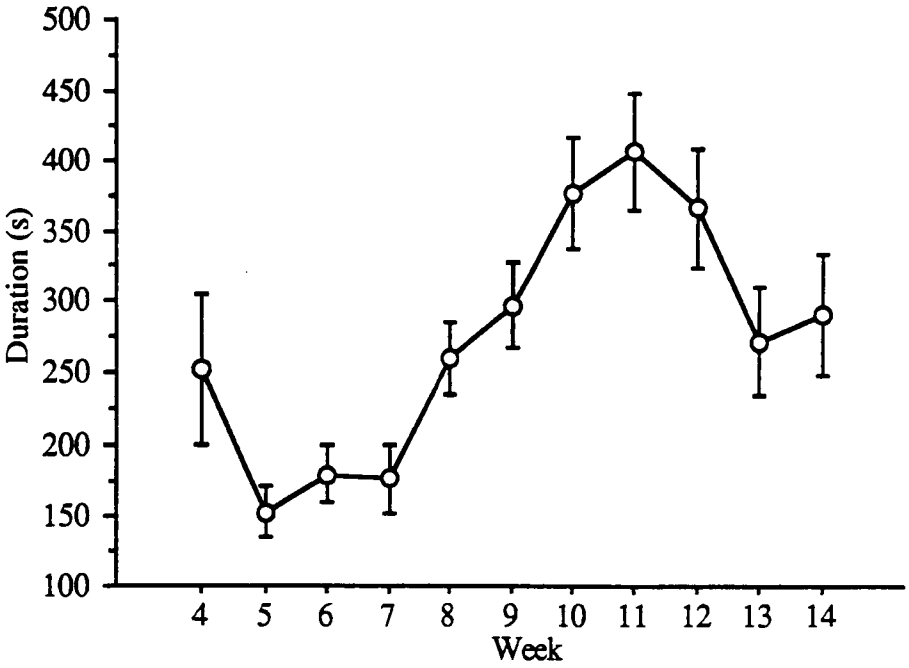

Figure 2-14. MBL +/- S.E. for sleep per week.

Table 2-5. Results of Fisher's PLSD between weeks for MBL of sleep.

Weeks	p	Weeks	p
4, 5	n.s.	7, 8	0.05
4, 6	n.s.	7, 9	0.01
4, 7	n.s.	7, 10	0.0001
4, 8	n.s.	7, 11	0.0001
4, 9	n.s.	7, 12	0.0001
4, 10	0.05	7, 13	0.05
4, 11	0.01	7, 14	0.05
4, 12	n.s.	8, 9	n.s.
4, 13	n.s.	8, 10	0.01
4, 14	n.s.	8, 11	0.01
5, 6	n.s.	8, 12	0.05
5, 7	n.s.	8, 13	n.s.
5, 8	0.01	8, 14	n.s.
5, 9	0.0001	9, 10	n.s.
5, 10	0.0001	9, 11	0.05
5, 11	0.0001	9, 12	n.s.
5, 12	0.0001	9, 13	n.s.
5, 13	0.01	9, 14	n.s.
5, 14	0.01	10, 11	n.s.
6, 7	n.s.	10, 12	n.s.
6, 8	0.05	10, 13	0.05
6, 9	0.01	10, 14	n.s.
6, 10	0.0001	11, 12	n.s.
6, 11	0.0001	11, 13	0.01
6, 12	0.0001	11, 14	0.05
6, 13	0.05	12, 13	n.s.
6, 14	0.05	12, 14	n.s.
		13, 14	n.s.

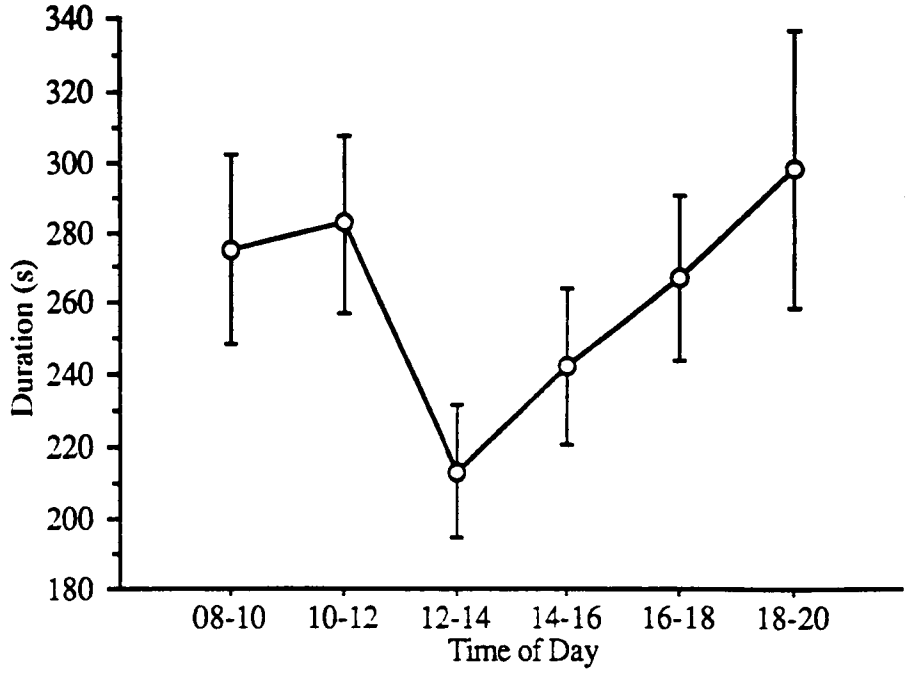

Figure 2-15. MBL +/- S.E. for sleep per time of day.

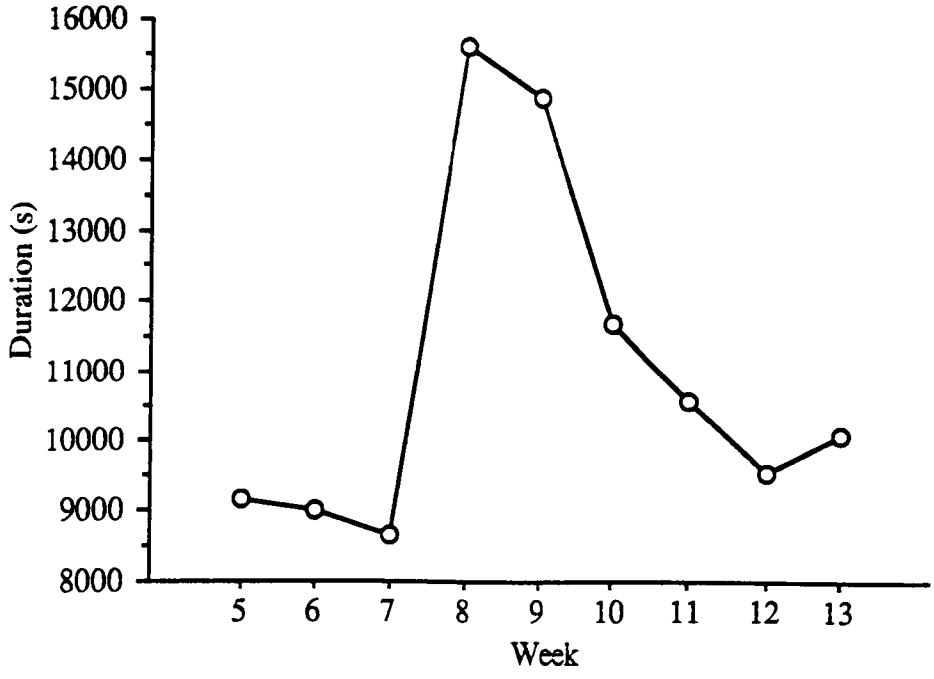

Figure 2-16. Total amount of time spent sleeping per week.

Table 2-6. T-test values between categories for MBL of sleep.

Individuals	Mean Diff.	DF	t-value	p
(a). Before separation from the mother.				
F, M	53.584	327	2.270	n.s.
1F, 2F	60.076	95	1.427	n.s.
1M, 2M	-27.438	102	-0.709	n.s.
1M, 3M	-11.506	106	-0.306	n.s.
1M, 4M	49.742	122	1.515	n.s.
2M, 3M	15.392	106	0.419	n.s.
2M, 4M	77.180	122	2.325	0.05
3M, 4M	61.248	126	1.901	n.s.
(b). After separation from the mother.				
A, F	27.733	49	0.409	n.s.
A, M	55.338	86	0.974	n.s.
A, J	33.480	117	0.584	n.s.
F, M	27.605	99	0.576	n.s.
1F, 2F	231.325	30	2.886	0.01
1M, 2M	68.853	38	0.991	n.s.
1M, 3M	77.872	33	1.220	n.s.
1M, 4M	-124.619	24	-1.473	n.s.
2M, 3M	9.019	41	0.139	n.s.
2M, 4M	-193.471	32	-2.211	0.05
3M, 4M	-202.490	27	-2.527	0.05

A=all adults, F=all females, J=all juveniles, M=all males, Mean Diff.= mean difference between individuals in s., DF=degrees of freedom.

Juveniles would sleep in any position (e.g. on their back; dorso-ventrally extended; on their side; curled into a ball, etc.). There seemed to be no preferred position. Also, sleeping was maintained during disturbances, such as one juvenile walking on top of a sleeping animal or soliciting play.

Interactions Between Siblings

Play began at around 41 days, just after the eyes opened. Before this time individuals were seen biting each other, which in retrospect resembles some of the play biting observed later, and therefore could be the onset of play behaviors. Behaviors are listed and described in Table A-2.

MBL for play was 23.608 s (n=384, s.d.=38.095). It peaked in week 7 and then decreased with time (Figure 2-17). Each individual followed the same basic pattern, though 2M did not play at all in week 7 and had a significantly higher duration in week 8 (Figure 2-18). There is a significant difference in MBL among weeks ($F=12.204$; d.f.=9, 374; $p<0.0001$). Looking at differences between weeks (Table 2-7), several groups emerge that are similar to each other, but different than other weeks: 5-8 and 10-14, with week 9 being different from all other weeks except 5 and 8.

Play duration was longest in the late afternoon and approximately equal at all other times (Figure 2-19). The total amount of time spent playing also peaked in week 7 and decreased

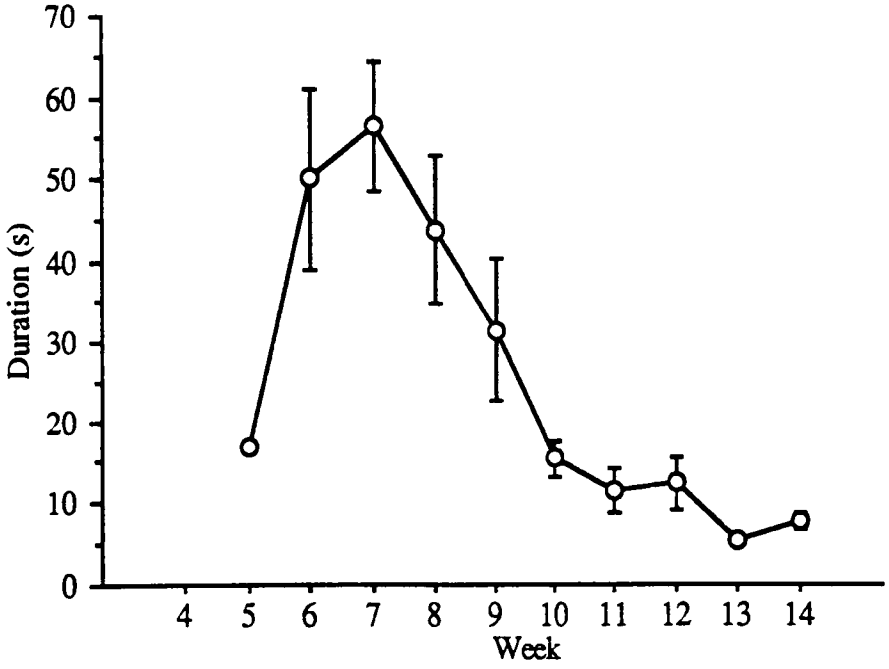

Figure 2-17. MBL +/- S.E. for play per week.

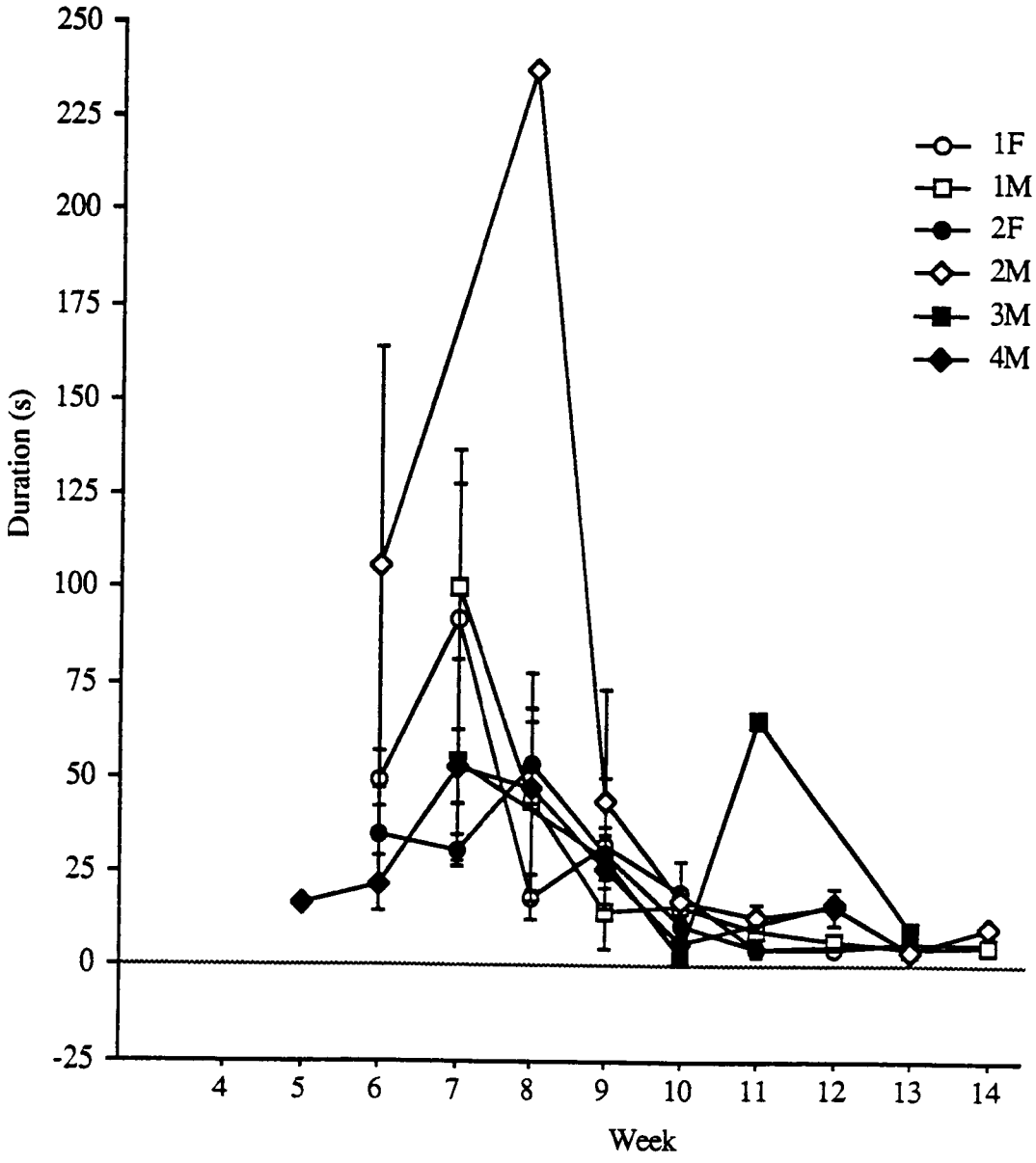

Figure 2-18. MBL +/- S.E. for play per week of individual juveniles. Open symbols represent ermine housed together after separation; closed symbols represent ermine housed separately after separation (see text for further explanation).

Table 2-7. Results of Fisher's PLSD between weeks for MBL of play.

Weeks	p	Weeks	p
4, 5	---	7, 8	n.s.
4, 6	---	7, 9	0.01
4, 7	---	7, 10	0.0001
4, 8	---	7, 11	0.0001
4, 9	---	7, 12	0.0001
4, 10	---	7, 13	0.0001
4, 11	---	7, 14	0.0001
4, 12	---	8, 9	n.s.
4, 13	---	8, 10	0.0001
4, 14	---	8, 11	0.0001
5, 6	n.s.	8, 12	0.001
5, 7	n.s.	8, 13	0.0001
5, 8	n.s.	8, 14	0.0001
5, 9	n.s.	9, 10	0.05
5, 10	n.s.	9, 11	0.05
5, 11	n.s.	9, 12	0.05
5, 12	n.s.	9, 13	0.01
5, 13	n.s.	9, 14	0.01
5, 14	n.s.	10, 11	n.s.
6, 7	n.s.	10, 12	n.s.
6, 8	n.s.	10, 13	n.s.
6, 9	0.05	10, 14	n.s.
6, 10	0.0001	11, 12	n.s.
6, 11	0.0001	11, 13	n.s.
6, 12	0.0001	11, 14	n.s.
6, 13	0.0001	12, 13	n.s.
6, 14	0.0001	12, 14	n.s.
		13, 14	n.s.

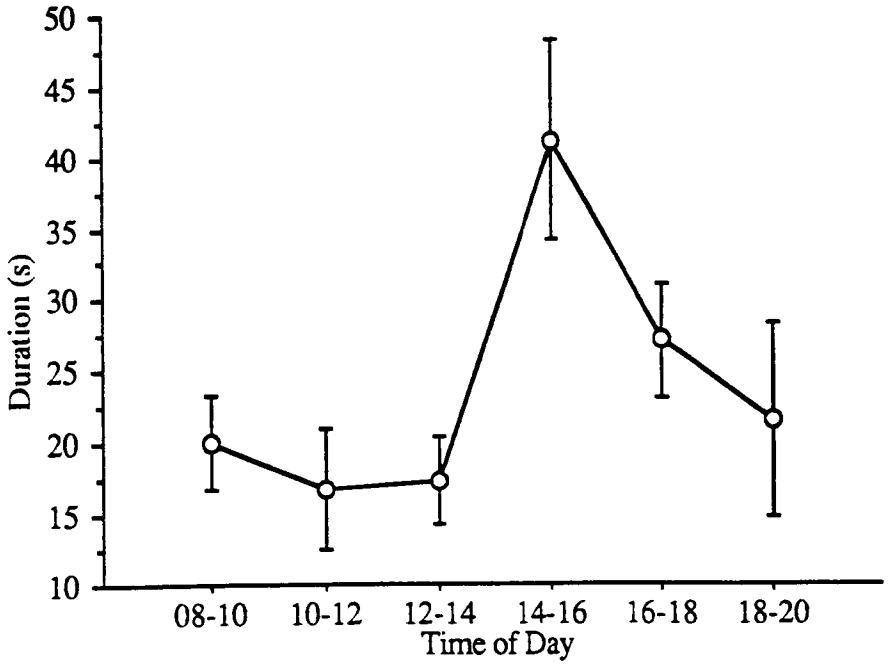

Figure 2-19. MBL +/- S.E. for play per time of day.

afterwards (Figure 2-20), though there was a sudden increase in play in week 10, similar to the increase in movement at this same time period. Before separation there were no significant differences in MBL among or between sexes, though after separation 4M had a significantly higher MBL than 1M and 2M (Table 2-8). However, this result is suspect, as a graph of MBL shows that 4M does not differ significantly from the other juveniles (Figure 2-18).

Certain individuals played with each other more than with other siblings (X^2=27.836, d.f.=14, $p<0.05$). 3M and 2F never played with each other, 1F and 2F played with each other the most, and 1M and 3M and 1M and 1F played minimally. No stable dominance hierarchy was observed during play, and associations did not seem to be sex-biased, though this could not be definitively proven. Based on an analysis of proximity at the beginning of each observation day, individuals did not appear to associate preferentially with any other siblings (X^2=6.28, d.f.=14, $p>0.05$).

Intense aggression (as defined in Table A-1) was never observed. However, the play behaviors began to be more forceful and aggressive beginning around 60 days. The juveniles seemed to bite more and the bites seemed to be stronger. There was also much more vigorous activity, such as chasing, wrestling, and running when moving around the cage. Chasing became common around 65-70 days, especially with the trio (1M, 2M, 1F) after separation from the mother.

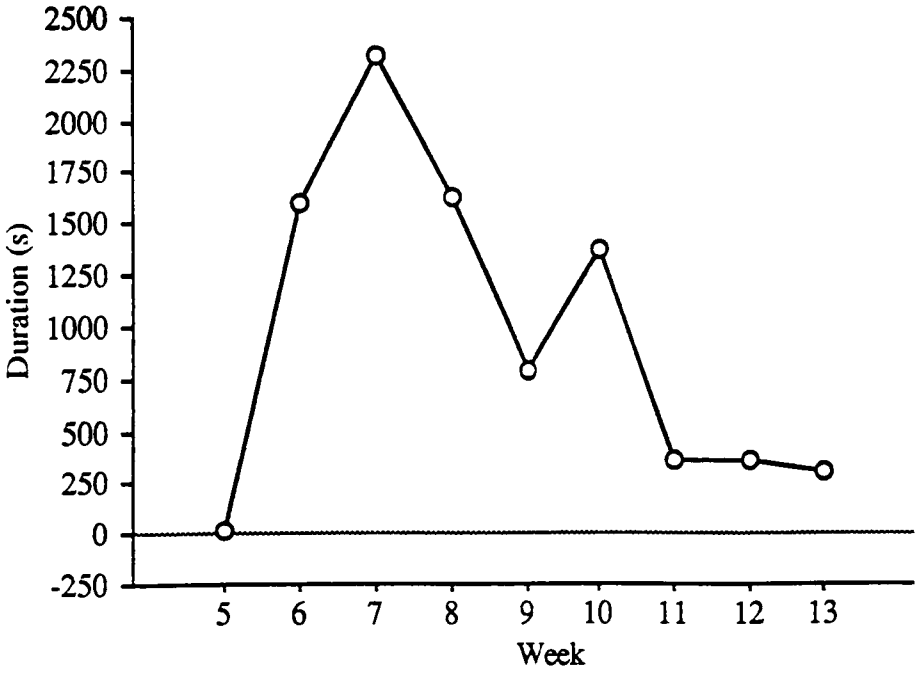

Figure 2-20. Total amount of time spent playing per week.

Table 2-8. T-test values between categories for MBL of play.

Individuals	Mean Diff.	DF	t-value	p
(a). Before separation from the mother.				
F, M	1.579	226	0.271	n.s.
1F, 2F	-6.562	82	-0.827	n.s.
1M, 2M	-5.178	89	-0.453	n.s.
1M, 3M	-15.071	38	-0.938	n.s.
1M, 4M	-7.468	54	-0.711	n.s.
2M, 3M	-9.893	63	-0.436	n.s.
2M, 4M	-2.290	79	-0.173	n.s.
3M, 4M	7.603	28	0.474	n.s.
(b). After separation from the mother.				
F, M	-8.073	154	-1.971	n.s.
1F, 2F	8.025	50	0.828	n.s.
1M, 2M	3.778	98	0.752	n.s.
1M, 3M	4.172	40	0.229	n.s.
1M, 4M	-30.525	46	-2.418	0.05
2M, 3M	0.393	64	0.060	n.s.
2M, 4M	-34.304	70	-5.885	0.0001
3M, 4M	-34.697	12	-2.015	n.s.

A=all adults, F=all females, J=all juveniles, M=all males, Mean Diff.= mean difference between individuals in s., DF=degrees of freedom.

Beginning at 54 days, mating attempts were observed among individuals, using proper mating positioning (mating attempts with adults were made at 41 days, see Chapter IV for details on mating posture). These bouts were sporadic in occurrence. Mating attempts were always found in the context of play. A play bout would segue into a mating attempt and usually then back into normal play; mating attempts were never isolated behaviors. Among individuals, 1M and 4M performed this behavior mostly to 2F and 2M and 3M mostly to 1F, though the overall number of attempts per male were approximately equal. Additionally, 1M mounted each of the other males, even mounting 4M on three different days. The other males never mounted a male, nor did any of the females.

Activity and Inactivity

To further analyze broad patterns of activity behaviors, movement and play were combined into a new category called "activity"; non-movement and sleep were merged into "inactivity".

MBL over the duration of a day for activity (Figure 2-21) shows little or no difference between time periods, though it is slightly higher in the morning. There is also little difference in the MBL of activity during ontogeny, though there is an increase in week 12 (Figure 2-22). Total activity time shows a similar pattern to MBL, with little change from week to week, though there is a jump in week 10 (Figure 2-23).

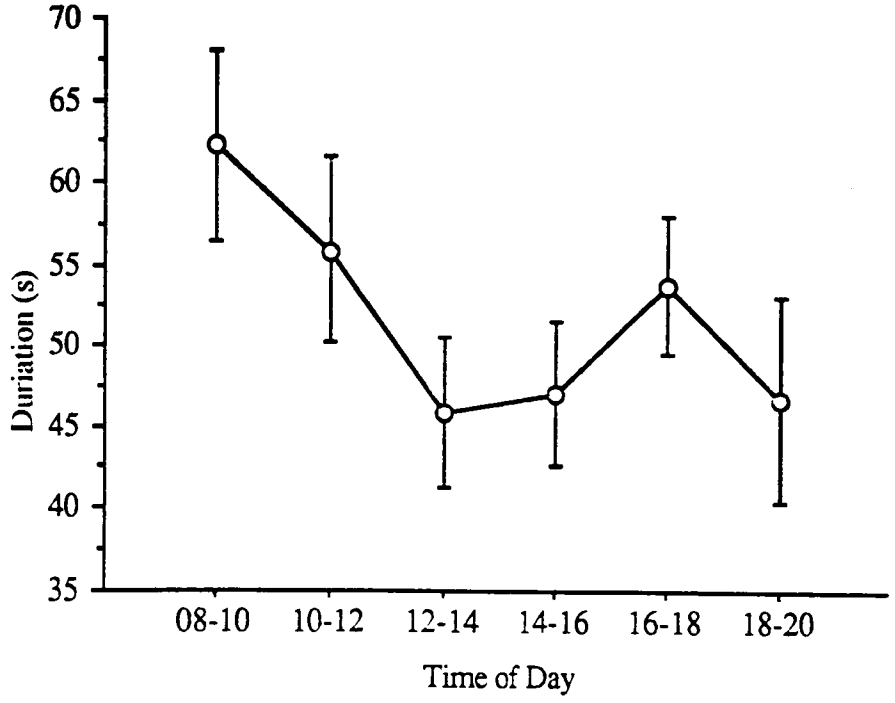

Figure 2-21. MBL +/- S.E. of total activity per time of day.

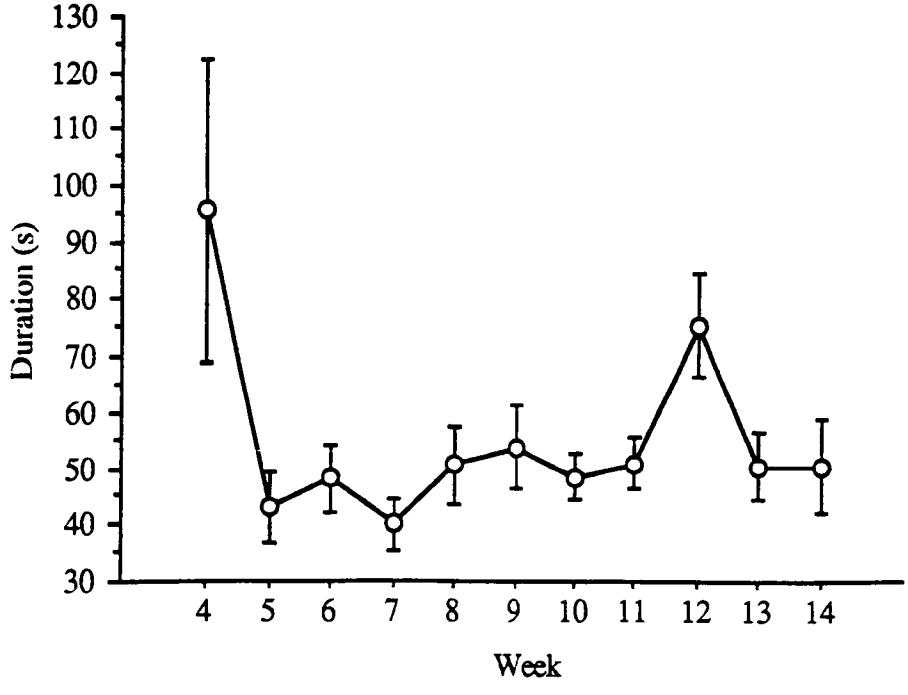

Figure 2-22. MBL +/- S.E. of total activity per week.



Figure 2-23. Total amount of activity per week.

MBL of inactivity shows that individuals are most inactive in the late morning and late evening (Figure 2-24). When plotted against weeks (Figure 2-25), there is no clear pattern, though weeks 5-7 are similar, as are 10-14, and there is a general decrease over time. The total amount of time inactive (Figure 2-26) shows a similar pattern to MBL. Weeks 5-7 are approximately the same, as are the weeks from 10 on.

Interactions With Mother

Juveniles began "mouth suckling" (Ewer, 1973) the adult female at 39 days. The positioning varied, though it usually involved the young approaching the mother and licking her lips with an open mouth. If her mouth was open, the young would additionally lick the inside of her mouth. Mostly, the mother seemed to be indifferent to this attention by the juvenile. Bouts averaged 63.723 s (n=6, s.d.=135.674). Ewer (1973) has speculated that this infrequently observed behavior has a two-fold function: to provide the young with gastrointestinal flora which will aid in digesting food before the young begin to provide their own flora, and to habituate young to a certain taste, namely the food that they should eat. See Chapter III for more details on this behavior.

Juveniles never played with the mother, though they made several attempts. A juvenile would approach the adult female and begin biting or pulling at her in the same way as soliciting a sibling

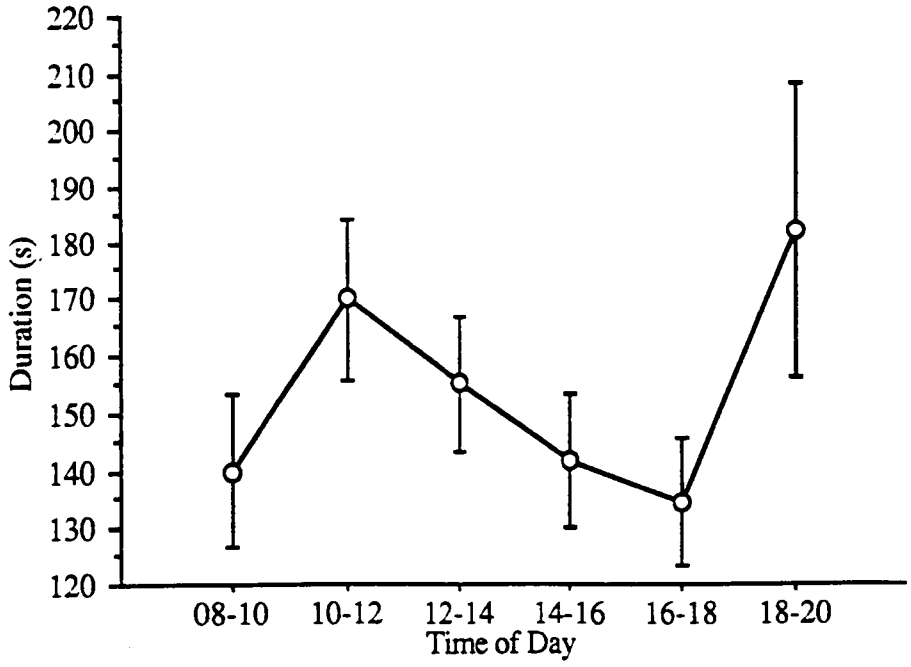

Figure 2-24. MBL +/- S.E. of total inactivity per time of day.

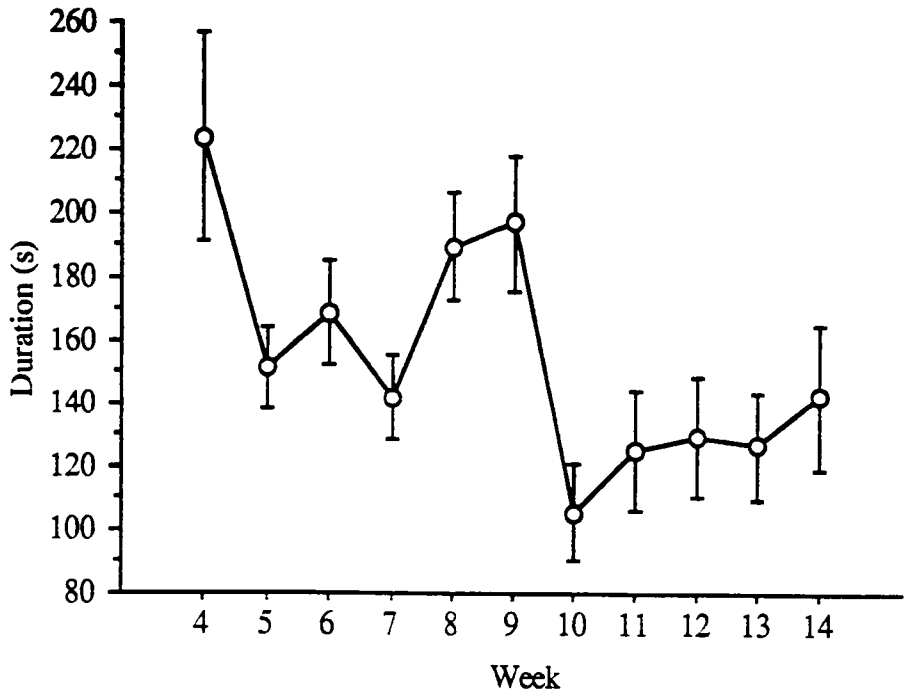

Figure 2-25. MBL +/- S.E. of total inactivity per week.

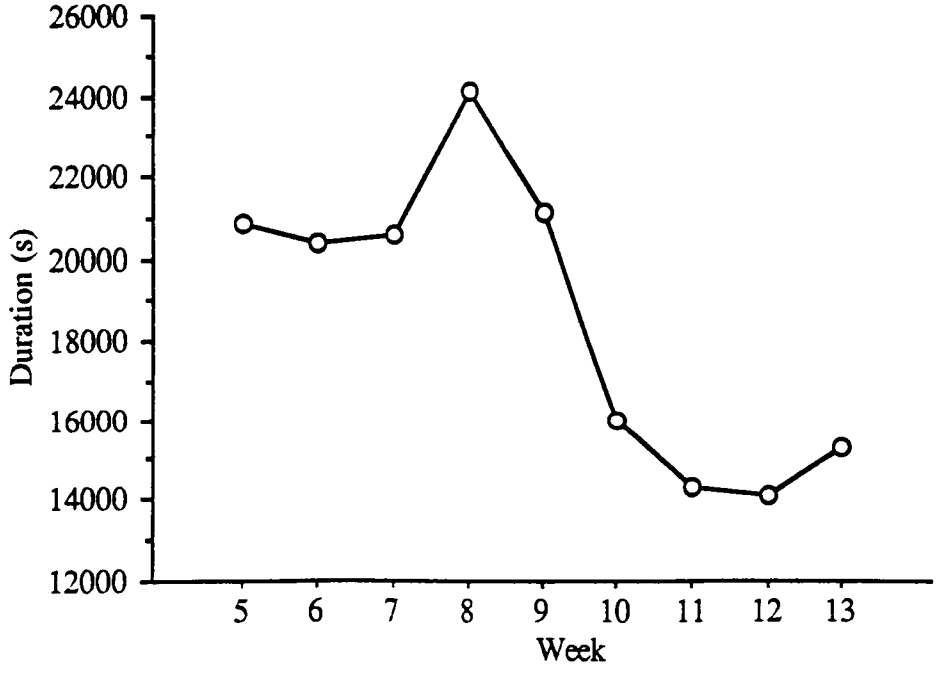

Figure 2-26. Total amount of inactivity per week.

to play. Invariably, the mother would ignore this behavior, often walking away from the juvenile. If the mother simply lay still, the juvenile would cease the attempts after a few seconds.

Feeding and Maintenance

Observations began at about the time when the juveniles should have terminated lactation (King, 1989). Even so, nursing continued, though the actual number of bouts observed is small.

MBL for nursing was 32.173 s (n=14, s.d.=35.528). Nursing ran mostly through 42 days, though it was sporadic after 35 days. Most individuals stopped nursing about this time, though 3M was observed nursing until 77 days. Because of the small number of juveniles, it was impossible to determine inter-suckling intervals. Additionally, the "milk-tread" or "rooting" behaviors seen in many carnivores (Ewer, 1973) was never observed. An individual would approach the mother, place its mouth on her ventrum, move the head until a nipple was located, then begin suckling. Only one individual was observed suckling at a time.

Eating of solid food was first observed at 35 days, though it may have occurred sooner. MBL for eating solid meat was 63.348 s (n=62, s.d.=70.205). Initially the young chewed with the front of their mouth, seemingly using only incisors. By 43 days they were still using mainly the front portion of the mouth, though it seemed

they were beginning to use the carnasials. Fully adult eating patterns were seen by about 80 days.

Juveniles began performing grooming behavior at about 42 days. This behavior was seen infrequently and lasted a mean of 19.054 s (n=14, s.d.=29.889).

Vocalizations

As a whole, juveniles rarely vocalized. Even play was conducted in relative silence. The most common occurrence of vocalizations was when the juveniles were startled or alarmed by disturbances (noises, sudden movements, etc.). Vocalizations observed are described below. Huff and Price (1968) and Hartman (1964) observed four vocalizations in *M. nivalis*: chirp, hiss, scream, and trill .

Chirp--high-pitched, short, single-note call when startled or alarmed.

Chirrup--low, warbling sound when playing. Very infrequently observed.

Chortle--soft, "chortling" sound as crossing the cage or when near the mother; similar to adult trill (see Chapters III and IV).

Scream--Extended squeal.

Squeal--short, loud, warbling squeak when agitated (picked up by the mother, mating with an adult).

Interactions Among Behaviors

An analysis of covariation among play, movement, non-movement, and sleep durations produced some unusual results (Table 2-9). Overall, there are small but significant negative correlations between movement and both non-movement and play. There is a larger and more highly significant positive correlation between non-movement and play. More detailed analyses show that most individuals show no significant correlation between non-movement and movement, though when combined as sexes, the correlation becomes significant. The correlation between non-movement and play seems to lie with 1M and 4M, while the correlation between movement and play seems to lie with 1F. In females (specifically 2F) and males (except 3M) there is a large but insignificant correlation between sleep duration and play duration. Samples were too small in 1F and 3M to produce results, and too small in the others to give p-values.

A multiple regression among each of the four primary behaviors (movement, non-movement, sleep, and play) shows no interactive effects when each behavior is analyzed as a dependent variable against the remaining variables (sleep: $F=1.240$, n.s.; non-movement: $F=1.210$, n.s.; movement: $F=0.364$, n.s.; play: $F=0.448$, n.s.); furthermore, any influences are weak at best (sleep $R^2=0.347$; non-movement $R^2=0.341$; movement $R^2=0.135$; play $R^2=0.161$). These suggest that the behaviors do not significantly influence each

Table 2-9. Correlation values between selected behaviors.
S=sleep, NM=non-movement, M=movement, P=play

Behavior	n	r	p	n	r	p	n	r	p
		All Juveniles			**All Females**			**All Males**	
S, NM	301	-0.028	n.s.	85	-0.143	n.s.	216	0.022	n.s.
S, M	151	-0.084	n.s.	43	-0.133	n.s.	108	-0.079	n.s.
S, P	13	-0.221	n.s.	4	-0.785	n.s.	9	0.038	n.s.
NM, M	656	-0.116	0.01	198	-0.153	0.05	458	-0.096	0.05
NM, P	176	0.317	0.0001	68	-0.017	n.s.	108	0.492	0.0001
M, P	298	-0.119	0.05	116	-0.230	0.05	182	-0.050	n.s.
		1F			**2F**			**1M**	
S, NM	40	-0.223	n.s.	45	-0.128	n.s.	50	0.005	n.s.
S, M	19	-0.158	n.s.	24	0.187	n.s.	25	0.146	n.s.
S, P	1	---	---	3	-0.787	---	3	0.869	---
NM, M	67	-0.224	n.s.	131	-0.114	n.s.	139	-0.031	n.s.
NM, P	28	-0.112	n.s.	40	0.173	n.s.	38	0.655	0.0001
M, P	60	-0.275	0.05	56	-0.151	n.s.	65	-0.054	n.s.

Table 2-9. (continued)

Behavior	n	r	p	n	r	p	n	r	p
		2M			3M			4M	
S, NM	54	0.073	n.s.	56	0.170	n.s.	56	-0.146	n.s.
S, M	29	-0.088	n.s.	29	-0.129	n.s.	25	-0.178	n.s.
S, P	3	0.948	---	0	---	---	3	0.999	---
NM, M	104	-0.015	n.s.	121	-0.103	n.s.	94	-0.245	0.05
NM, P	41	0.185	n.s.	8	0.671	n.s.	21	0.532	0.05
M, P	86	-0.012	n.s.	9	-0.439	n.s.	22	-0.099	n.s.

other, and the bivariate correlations are likely not affected by a third behavior.

Discussion

Ermine, and other members of the genus *Mustela*, have a very rapid physical development whose pattern is unusual compared to other carnivores. Most carnivores gain weight steadily during ontogeny (arctic fox, *Alopex lagopus*: Wakely and Mallory, 1988; bush dog, *Speothos venaticus*: Kitchener, 1971; coyotes, *Canis latrans*: Bekoff and Jamieson, 1975; domestic cat, *Felis sylvestris catus*: Baerends-Van Roon and Baerends, 1979; Martin and Bateson, 1988; maned wolf, *Chrysocyon brachyurus*: Brady and Ditton, 1979). Ermine, and other weasel species, show a very rapid development occurring shortly after the eyes open (East and Lockie, 1965; Heidt *et al.*, 1968; Heidt, 1970; King, 1989), faster than most other carnivores (Ewer, 1973; Gittleman and Oftedal, 1987).

The central behaviors of young ermine (movement, non-movement, sleep, and play), remained fairly constant with little variation between weeks, up until week 7 or 8 (though observations were not made before week 4). After this point in time the behaviors shift. The reason for this is likely linked to the ontogeny of locomotion in the juveniles. Full adult locomotor capabilities are

attained in week 7, allowing them to move around more; indeed, movement increases and non-movement decreases after this time. Domestic cats (*Felis sylvestris catus*) show a similar pattern of development, increasing the activity rate shortly after adult-like locomotion is attained in weeks 6-7 (Martin and Bateson, 1988).

There are two other periods of time that signal behavioral changes. One is week 10, where there is an unexpected increase in activity. Also during this week the juveniles are spending less time in the nestboxes and therefore more time in the cage. It is likely that this increase in activity is triggered by natal dispersal. In the wild ermine disperse at about 3-4 months (King, 1989). And though these behaviors occur several weeks before the wild dispersals, it is not unlikely for this to be the reason. There is much variation in the dispersal times within carnivore species (Gittleman, personal communication), possibly allowing for this seemingly early dispersal.

The other time period is week 12, in which there is an increase in both MBL and total duration of movement. This increase is likely because the young are suddenly exposed to a new environment and spend much of their time exploring. This hypothesis is supported by the fact that MBL and total duration begin decreasing again after week 12. If the flurry of action is an initial reaction to a novel environment, then it should decrease as the animals become acclimated to the novelty, which it does.

The MBL of the activity behaviors remains constant or even decreases over time. However, the total durations of these behaviors

(particularly movement) increase steadily during ontogeny. This suggests that the bouts become shorter but are more frequent at the ermine age. The inactivity behaviors (sleep and non-movement) decrease in both MBL and total frequency, again suggesting that the ermine become more as they age. This pattern of activity increasing with age is shown in other carnivores (Brady and Ditton, 1979; Martin and Bateson, 1988; Ortega, 1988).

Though these general patterns of activity and behaviors hold true among carnivores, the actual emergence time of the behaviors and the timing of certain physiological changes (e.g. eyes opening) can differ greatly and in unexpected ways. Though ermine have one of the most rapid growth rates of carnivores (Gittleman and Oftedal, 1987), their eyes open relatively late, at around 35-40 days (Ewer, 1973; King, 1989). By contrast, otters' eyes open between 28-35 days (Chanin, 1985), canids' around 14 days (Bekoff and Jamieson, 1975), domestic cats' within the first two weeks (Martin and Bateson, 1988), lions' between the third and 15th day (Schaller, 1972), and spotted hyenas who are born with their eyes open (Kruuk, 1972). Onset of play behaviors in ermine is also delayed in comparison to other mammals. In this study, young began playing around 41 days, while crab-eating foxes begin around 17 days (Brady, 1978), maned wolves around 21 days (Brady and Ditton, 1979), squirrels around 37 days (Gurnell, 1987), and domestic cats around 28 days (Martin and Bateson, 1988).

Despite these initial delays, once behaviors emerge, they develop at an almost exponential rate. They are weaned at around 4-5 weeks, compared to 12 weeks in badgers (Neal, 1986), 7 weeks in otters (Chanin, 1985), and 8-9 weeks in lions (Schaller, 1972). Ermine also disperse early, at 3-4 months (King, 1989), while many other carnivores remain with the natal group for several years (Mech, 1970; Kruuk, 1972; Schaller, 1972; Ewer, 1973). This latter observation may seem moot, in the light that most other carnivores are larger than ermine and therefore would take longer to reach adult size, but these are the same animals who have features which develop earlier than ermine (as mentioned above). This contrast underscores the extreme rate of development of ermine.

Among individuals, 4M stands out as being different from his siblings after separation. According to t-statistics, he shows a higher MBL than most of the other males in movement, sleep, and play, and a lower MBL in non-movement, suggesting a higher overall level of activity. These results are unusual for a number of reasons. First, he has a higher MBL in play, even though he is housed individually and has no physical contact with any other ermine. Therefore this play is entirely object play (with a mouse or materials in the exhibit). This same male is also consistently the heaviest male. It is possible that this increased size is related to a higher activity level, though this difference does not stand out until after separation. It must be noted, however, that this same difference does not show up in a graph of play durations, making the t-statistics suspect.

Assuming a real difference exists, the presence of siblings could have an inhibitory affect on 4M's behavior, though a seemingly more likely explanation could be linked to competition for food resources among juveniles, as explained below. Siblings can have an influence on each other's behaviors, as in domestic cats (Bateson and Young, 1979)

A similar pattern to 4M can be seen in 2F. She has a lower MBL of sleep and non-movement after separation than 1F, and is consistently the heaviest female. Reasons for her behaviors could be the same as for 4M.

Both 4M and 2F are housed individually, yet have higher levels of activity than their siblings being housed together, though it would seem that those housed together would have more potential for interaction and play, and therefore more activity. The results observed are contrary to this hypothesis. The ermine kept together (1M, 2M, 1F) are also lighter than their siblings. These weight differences are especially pronounced after week 12. The weight differences could be explained by the individually housed ermine not having to compete with siblings for food. Any mice they have they eat without having to fight for it. The ermine kept together could have had to compete against each other for the mice present. This difference in weight could also possibly explain the activity differences. The ermine who compete have less resources and therefore might not be as well nourished as the individually housed ones, and because of this might show a decreased activity level.

This hypothesis, that the undernourished ermine have a lower activity level, is supported by other studies. Collier *et al.* (1972) found that in rats a reduction in weight produced a decrease in activity level. Richardson (1973) studied two related species of shrews and determined that the smaller species had a lower activity level than the larger one. These ideas fit the data for the ermine. Juveniles who compete for food eat less and are therefore lighter and smaller, decreasing activity levels. This hypothesis could be tested by determining whether the juveniles actually compete for food, and seeing if there are behavioral differences between normally fed and undernourished animals. It is also likely that these animals exhibit greater durations and frequencies of play behavior because of the captive environment. They are not required to hunt for food, leaving more time to engage in other behaviors, such as play. Also, being in captivity the are likely better fed and healthier than wild conspecifics, leading to increased activity and increased play (as the above discussion on activity levels and nutrition).

None of the behaviors seemed to correlate strongly with any of the mother's actions. The juveniles seemed to be acting of their own accord without influence from the mother. However this conclusion is based on the fact that the mother did not react strongly to any of the juveniles' behaviors and the juveniles seemed to pay little attention to her, except for reacting to alarm calls. It is also possible that most interactions with the mother occur before weaning, which

this study did not observe. The mother's behaviors and her reactions towards the young are dealt with in Chapter III.

It must be remembered that this study was conducted on only one litter of six individuals and therefore replication of these observations are needed. There are often wide-ranges of behaviors and patterns of individuals within a given litter (Fox, 1972), which can mask any overall patterns for the species. However, some of the behaviors studied here, namely movement, non-movement, sleep, and play, are broad enough to use for making general assumptions of the behavior of juvenile ermine.

Chapter III

MATERNAL CARE

Introduction

Parents protect their young from a potentially harmful environment, regulate the onset of puberty and hormonal levels (Hofer, 1981; Rosenblatt and Siegel, 1981), teach them skills necessary for survival (Caro, 1980b; Asa, 1987; Lode, 1989), and help establish social bonds and patterns (Hofer, 1981; Swartz and Rosenblum, 1981). In general, more maternal care is provided in species with altricial young as opposed to precocial young (Eisenberg, 1981). For example, the mother usually prepares a nesting area, which involves considerable time and effort. After parturition, the female must keep the nest clean of wastes, and must often stimulate elimination by orally stimulating the infants' anogenital regions. The mother must also spend time with the young shortly after parturition to aid in thermoregulation, which in young is often not fully developed at birth. Precocial young, on the other hand, are able to move around on their own and fend for themselves in a matter of hours after birth (Ewer, 1968).

Ermine have a solitary life-style in which a single female is solely responsible for the care and defense of the young. The young are born quite small but grow rapidly, feeding almost exclusively for

the first month and a half of life on the mother's milk (King, 1989). This places considerable energetic costs on a female, as lactation is energetically expensive (Gittleman and Oftedal, 1987). Therefore, the mother is required to hunt often until the young can capture prey themselves. This is especially remarkable in the light of the adult's own rapid metabolism, requiring them to feed often, and making survival without food for more than a day or two very difficult (King, 1989). Because neonatal weasels are "expensive" to care for, they likely represent high parental investment compared to other carnivore species. Accordingly, a female should take steps to protect this investment, which should be evident in overall maternal care behaviors.

As with juvenile behaviors, data concerning maternal care in the genus *Mustela* are scarce. Considerable speculation exists on whether or not the mother teaches the young to kill or perhaps intends for them to observe her when she makes a kill. Some sources (East and Lockie, 1964; Heidt *et al.*, 1968; Heidt, 1970) describe events which are interpreted as teaching behavior, whereas others (King, 1989) seriously question these results. Again, it is surprising that few studies have looked at this aspect of behavior among weasels, considering the ease in caring for female ermine and young in captivity.

This chapter will generally describe and evaluate patterns of maternal behavior. Only behaviors directed toward the young are included. Many observed trends are subject to small sample size

effects, requiring future replication, and results are often inconclusive.

Methods

Subjects

Study subjects were the same as described in Chapter II.

Housing

Housing conditions were identical to those in Chapter II.

Observational Methods

Observations began on May 13, 1992 and continued until July 22. The adult female was observed with scan sampling (Altmann, 1974) at 1 m. intervals for a total duration of 60 m. Observations were made at different times each day on a rotating schedule, from 800-2000. Observations continued until the juveniles were separated from the mother.

Observations were recorded on a check-sheet by hand. On a given scan, the mother was categorized with respect to four variables: Location (cage or nestbox), asleep or awake, proximity (within one body length) to young, and whether she was moving.

Additionally, general comments were made between intervals on interactions with the young as well as general maternal behaviors. Analyses were conducted only on those behaviors related to the mother's interactions with or care of the young.

Results

Maintenance of Young

The mother directed little attention toward young other than direct maintenance or control. She did not play with them or engage in any activities that resembled "teaching". Her primary concern seemed to be keeping control of the young, particularly when they were less than 44 days old. She would pull juveniles back into a nestbox whenever they attempted to leave by grabbing them by the scruff of the neck, though they did not make many such attempts at that age. The initial presence of people would cause her to quickly drag any young in the cage area into a nestbox. By 55 days the adult female was spending less time in proximity to the juveniles and less time handling them. She seemed to almost ignore them except when they would lay in the entrance to a nestbox and she would pull them out of the way so she could enter and exit. After about 55 days she would also react less to the presence of humans (she would be less agitated and make fewer alarm calls). This pattern of ignoring the

young continued until separation from them at 77 days after parturition.

The mother did little to care for the young other than allowing them to nurse and bringing them into the nestbox when she presumably perceived danger (i.e. presence of humans; noise), and grooming and mouth-licking them. Only 4 bouts of grooming the young were observed. She also did not seem to provision the young with solid food or teach them to kill, as speculated previously (East and Lockie, 1964; Heidt *et al.*, 1968; Heidt, 1970). Live mice were not placed with the ermine, as approval was not granted by the Minnesota Zoo, but other adults were frequently seen grabbing dead mice in the stereotypical killing posture (grabbing the prey by the back of the neck and wrapping the ventrum around it [King, 1989]). Therefore the female had opportunity to teach the young using dead mice, though any such behavior is more likely to have been exhibited if live mice were used. She never solicited the young to nurse, they seeming to perform this behavior opportunistically and she remaining passive. Therefore beyond providing milk and defense, the mother seemed to provide little else in care of the young.

Associations with the Young

As mentioned above, the mother interacted directly with her young only infrequently. She never played with them, and in fact would ignore them or walk away when a juvenile would solicit play

(bite her, pull on her, roll on top of her, etc.). She also spent little time "handling" or carrying the young; only 22 instances were observed, these including moving the young back into a nestbox.

The mother spent an average of 76% of the observation periods in proximity to at least one young (x=45.652 scans out of a possible 60, n=46, s.d.=14.797). It is unclear whether this pattern changes significantly over the ontogeny of the young. There is an increase in week 6, then a decrease over the next two weeks followed by another increase (Figure 3-1). However, because of wide variation, there is no significant difference among the weekly means (F=1.567; d.f.=6, 39; n.s.) The total amount of time spent with the young shows a similar pattern (Figure 3-2).

One behavior that did stand out was "mouth suckling" as stated by Ewer (1973), but which seems more appropriate to be called "mouth licking". This occurs when the mother would lick a juvenile's mouth region, with the juvenile's mouth often slightly open. The reverse would also happen, as would a bout of mutual licking. The bouts lasted for a mean of 29.929 s (n=14, s.d.=60.147), and were spread fairly evenly among individual juveniles. Mouth licking was first observed at 33 days, but as this was the beginning of observations it may have been performed before this time. It continued through the ontogeny of the young, though remained sporadic.

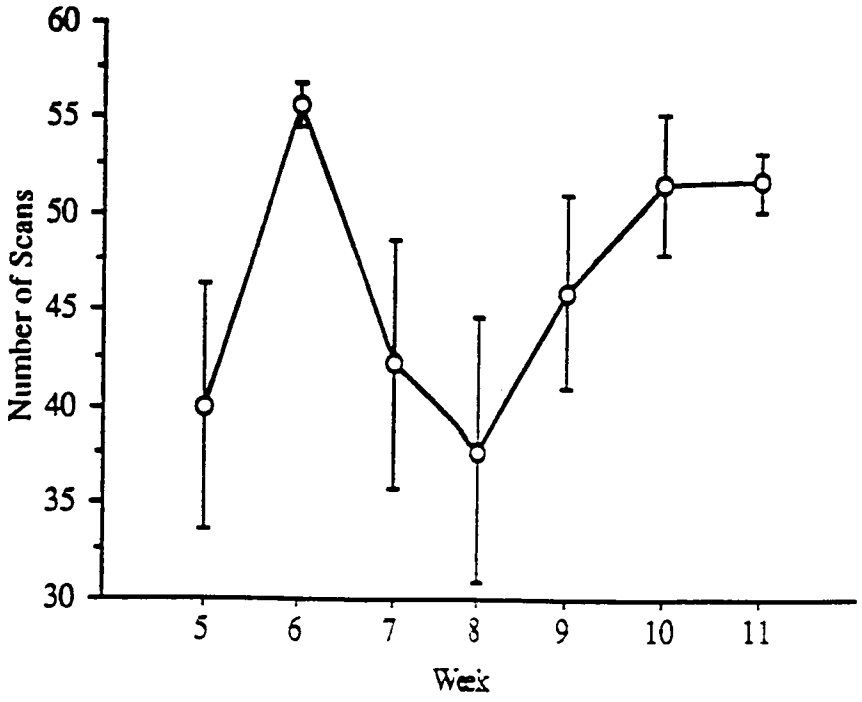

Figure 3-1. Average proximity of mother to at least one young.

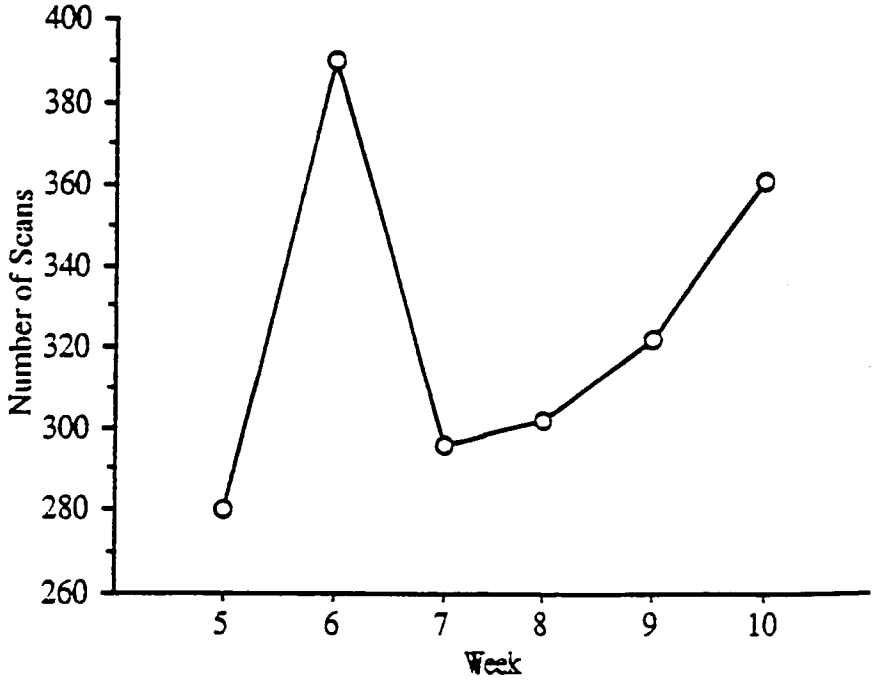

Figure 3-2. Total amount of time spent in proximity to at least one young per week.

Discussion

Ermine (and possibly other small mustelids) are unusual among carnivores in the minimal amount of maternal care given to young (i.e. types and durations of behaviors). Other carnivores perform such actions as vigilance for predators and prey (Caro, 1987), playing with the young (Caro, 1980b; Mendl, 1988), teaching them to hunt (Liers, 1951; Kruuk and Turner, 1967; Baerends-Van Roon and Baerends, 1979; Caro, 1980b; Lode, 1989), and providing them with food before they are able to fend for themselves (Brady, 1978). The fact that ermine do not seem to perform these actions, at least in captivity, is striking.

However, several factors must be kept in mind. This was a study with only one litter and therefore only one mother, making replication of this study in the future a necessity, to verify any results or trends. There could be much intraspecific variation in maternal care, which would not be shown in this study (and in fact has not been tested at all in this genus). Also, this study concentrated on the behavior and development of the young, the mother's behaviors being secondary. It is therefore possible that many of the subtleties of her actions were missed. Another problem is that most of the maternal behaviors mentioned in the introduction explicitly relate to the natural environment. These behaviors, namely predator vigilance, teaching of hunting, and providing for young, could not occur in captivity, as the appropriate stimuli are not

available. Therefore the behaviors would not be exhibited. These restrictions should be remembered in analyzing the data.

The mother did seem aware of possible threats to the young (i.e. human disturbances) and reacted to these by giving alarm calls and/or pulling the young into one of the nestboxes. Therefore, an increase in maternal care may be observed when young are threatened. She also showed little direct interactions with the young, often ignoring them when they would attempt to interact with her. There was little social interaction as a whole, which is not altogether unexpected in these animals, as they lead a solitary life.

It is possible that ermine young do not need the mother's instructions to learn communication skills necessary for reacting properly to conspecifics. These behaviors and signals can often be learned through play (Fagen, 1981). Ermine also have a rapid growth rate, which certainly reduces time available for the mother to teach the young. Because these animals lead such short lives (King, 1989) it would be beneficial for them to leave the nest as quickly as possible to be able to breed early in life. Therefore many stereotypical behaviors could have evolved with little learning required (such as hunting). The less time needed to learn skills, the quicker the animals can leave the nest. And if the young do not require teaching, the mother is left primarily to protect them from potential predators. This reasoning could explain the seeming lack of interest the mother shows towards the young. Primates (Nicolson, 1986; Walters, 1986) and social carnivores (Kruuk, 1972; Schaller,

1972) require more maternal care and a longer period as juveniles to learn social skills.

There are many behaviors common among carnivores that were not observed in the study animals. Many animals either bring parts of a kill to the young (Ewer, 1973; Brady, 1978; Baerends-Van Roon and Baerends, 1979; Deag *et al.*, 1988) or regurgitate food for the young (Mech, 1970; Ewer, 1973; Brady and Ditton, 1978). It is therefore unusual when a carnivore does neither, such as in spotted hyenas (Kruuk, 1972) and seemingly in ermine. Most carnivores also clean the young and stimulate elimination by licking the anogenital region (Ewer, 1973; Baerends-Van Roon and Baerends, 1979; Deag *et al.*, 1988), which was not observed in the study animals, though it could have been missed. Clearly, more detailed observations of the maternal behavior in this species, particularly in relation to ontogeny, must be made.

Chapter IV

NEONATAL BREEDING

Introduction

As mentioned in previous chapters, ermine have many unusual characteristics related to early stages of development. Probably the most extraordinary event of their ontogeny is neonatal breeding. This phenomenon has been described anecdotally in the lab and the wild (Ternovsky, 1983; DonCarlos *et al.*, 1986; King, 1989). It occurs when a female comes into estrous while she has a litter in the nest. A male will seek her out, mate with her, and at the same time mate with any juvenile females in the nest. It is believed that inseminated female neonates then give birth to healthy young the following year (DonCarlos, personal communication; DonCarlos *et al.*, 1986; King, 1989).

There are many questions surrounding this event. In relation to neonatal reproduction, the primary question is whether the adult males can differentiate between young of different sexes. Previous observations have determined that they do have this ability, and quickly discard juvenile males (DonCarlos, personal communication; King, 1989). Another question is whether the juvenile females are sexually mature upon mating with the adult males, and whether they will give birth the following year due to these matings. King (1989)

reports that females become sexually mature at 28-42 days, while males become sexually mature at around 360 days. This early maturation of the female, combined with delayed implantation, could make successful mating of the juveniles possible.

This chapter will look at the phenomenon of neonatal breeding. Emphasis will be placed on determining if the adult males can discriminate between sexes and if they show a preference for one, as well as describing the general behaviors associated with mating the juveniles.

Methods

Subjects

The adult female and juveniles were the same as mentioned in Chapter II. Additionally, three adult males were used in breeding introductions. All three were captive born at the Minnesota Zoo. Adult Male 1 (AM1) was 7 years old at the time of the breedings, had been bred in 1989 and 1990, both times without producing a litter, and was having health problems. Adult Male 2 was 4 years old at the time of the breedings and had never been mated previously. Adult Male 3 was 3 years old at the time of the study, had been bred the previous year, and was the father of the litter.

Housing

Adult males were housed according to procedures described by DonCarlos *et al.* (1986). All others were housed as mentioned in Chapter II.

Observational Methods

Before introduction of an adult male, the adult female and juveniles were locked into the nestboxes, preventing them access to the cage. Individuals were herded into whichever nestbox was closest, resulting in some juveniles being separated from each other and the adult female. A male was then placed in the cage in a transfer box (see DonCarlos *et al.*, 1986 for a description) and the cage secured. The female and juveniles were allowed access to the cage again and a male was released from the transfer boxes using a long wire to open their doors. Additional prodding and tipping of the transfer boxes was required to get AM2 and AM3 out of the box.

All animals were given free access to interactions within the cage and all bouts were videotaped with a hand-held video camera. However, the goal of the Minnesota Zoo was to have successful breedings. Therefore, two of the trials were manipulated. After AM2 was chased by the adult female (see below), she was locked in a nestbox, denying her access to him and the litter. After AM2 made repeated attempts to mate with juvenile males, those males were locked out, giving AM2 access to only juvenile females. AM3 was

also denied access to juvenile males after repeated mating attempts with them.

Introductions began at approximately 1100 on the 41st day after parturition, similar to previous neonatal breeding attempts (DonCarlos *et al.*, 1986). Males were allowed to remain in the cage until successful copulation was observed and/or a male ceased copulatory attempts. Males remained in the cage approximately 45 minutes each.

Females believed to have been inseminated were checked for sperm. They were immobilized without anesthesia and a sample of vaginal fluid removed with a pipet. This fluid was examined under a microscope for the presence of sperm. Previously at the Minnesota Zoo, the presence of sperm in the vagina indicated that the female would give birth to a litter the following year (DonCarlos, personal communication).

Results

General Behaviors

The position for mating is very stereotypical in ermine (King, 1989). The male bites a potential mating partner by the scruff of the neck with its teeth. He then wraps himself around the partner with his ventrum against their back, curving his body, so that both are

facing in the same direction and the male is holding the partner in the curve of his body. This positioning may be referred to as "spooning". A receptive female would move her tail out of the way of the anogenital region, allowing the male access. A stroking or "swimming" (DonCarlos, personal communication) motion with a hind leg by the male was indicative of penetration. Adult males would mate in this position with both the adult female and the juveniles of both sexes.

Two types of vocalizations occurred during the mating attempts. The first was a "trill", usually performed by the adult male. A trill was a low, soft cooing sound, similar to a dove. Trilling has been previously noted as being related to breeding situations (Huff and Price, 1968; DonCarlos *et al.*, 1986). The adult males, and possibly the adult female, also performed a sound similar to the juvenile chirrup (see Chapter II). It was often difficult to determine from which animal the sound was originating, as the sounds were quick, quiet, and the animals were usually moving in close proximity to each other.

Generally the adult female did not attempt to interfere with the adult males' mating attempts with the juveniles. She was usually in close proximity and would sometimes nudge or pull slightly on the male with her teeth, but would rarely try to pull the male or juvenile away or otherwise interfere with the attempt. A notable exception occurred when AM2 was roughly and improperly handling a juvenile female. He grabbed her by the neck, as in previous attempts, and

proceeded to attempt the copulatory position. The juvenile resisted and began twisting in his grasp. He began twisting around her, thrashing her about, grabbing her with his hind legs and attempting to copulate. The juvenile began making shrill alarm calls., and within seconds, the mother began pulling at the juvenile and scratching at AM2. Quickly her actions became more excited until she had pulled the juvenile away. She then chased the adult male around the cage for several seconds in a flurry of activity accompanied by a release of scent glands. The male retreated to an empty nestbox until the female stopped chasing him and did not return to the side with her nestbox and the juveniles. The adult female was separated from the male and AM2 allowed access to the juveniles. Further mating attempts with the juveniles went smoothly. Also, the female showed no change in reaction when the next male (AM3) was placed in the cage approximately 30 minutes later.

The juvenile females did seem to solicit a response from the adult male. They would often sniff the adult male's urogenital region and follow him around the cage, often in a clumsy manner. The juvenile females would also crawl over his body, primarily in the head region. This behavior was performed only by juvenile females, and not by the juvenile males or the adult female. Muller (1970) and DonCarlos *et al.* (1986) report similar behaviors of the juvenile females, including the emission of "high-pitched trills and chuckles" (King, 1989: 144) which develop into the adult trilling sound typically associated with mating behavior.

Table 4-1 shows the MBL for mating attempts of each of the adult males. Only AM3 successfully inseminated the adult and juvenile females. These successes most likely occurred on a 120 s duration mounting of 1F and a 350 s mounting of the adult female.

Preferences of Adult Males

The frequency of mating attempts are summarized in Table 4-2. AM1 seemed to show a mostly equal or random choice in partners. AM2 was approximately equal between juvenile females and juvenile males when there was equal opportunity to mate with either. Taking into account the increased male:female ratio among the juveniles, there seemed to be a bias towards juvenile females. AM3 made more mating attempts with juvenile males until they were locked out.

Adult males did not exhibit an ability to distinguish between juvenile males and females. All adult males made several mating attempts with the juvenile males. Both AM2 and AM3 made several attempts with the same male, often after already having sniffed the urogenital region or just making a mating attempt with the same individual!

Table 4-1. Mean bout length in seconds and standard deviation of the mating attempts of each adult male towards the other subjects.

Male	MBL	s.d.	MBL	s.d.	MBL	s.d.
	Juvenile	**Females**	**Juvenile**	**Males**	**Adult**	**Female**
AM1	20.40	6.68	18.67	9.46	29.00	15.56
AM2	61.89	87.24	43.60	52.60	0.00	---
AM3	32.75	35.66	12.50	3.50	108.50	140.09

Table 4-2. Number of mating attempts of each male towards the various study subjects.

Male	Juvenile Females	Juvenile Males	Adult Female
AM1	5	3	5
AM2	9*	5**	0
AM3	8***	4	4

* Four of these bouts occurred after the adult female was removed. Of the remaining ones, 3 occurred after the juvenile males were removed.

** All of these bouts occurred after the adult female was removed.

*** Six of these bouts occurred after the juvenile males were removed.

Discussion

Neonatal breeding has not been described in any other mammalian species. Badgers (*Meles meles*) have been known to give birth "early", within 8-9 months after parturition, but the breedings do not occur until several months after birth, usually about 7-8 months old (Neal, 1986). Some captive wolves have begun breeding at 10 months, though normal time for first breeding is 22 months (Medjo and Mech, 1976). Ermine have a much earlier onset of breeding, which has not been observed in any other members of *Mustela*. The closest parallel is the longtail weasel (*Mustela frenata*), in which the females can mate at 3-4 months, though by this time the juveniles are weaned and almost fully grown (King, 1989).

It is therefore likely that ermine breed at an unusually early age. Ermine have a short life-span, typically only 4 years, and a high mortality rate (King, 1989). Therefore, a rapid reproductive output would compensate this mortality pattern (Gittleman, 1993). Most members of the genus *Mustela* have obligatory delayed implantation (Ewer, 1973; King, 1989), which causes them to give birth in the year following mating. Such a mechanism is beneficial in a region where the growing season is short, for it ensures that ermine give birth when conditions are best for raising the young. Without delayed implantation, if an ermine was implanted in the spring and gave birth the same year, the litter might not be mature enough to care for themselves when winter came.

This mechanism could have been modified through natural selection to encompass neonates. If an animal with obligatory delayed implantation (i.e. ermine) were to become sexually receptive when its mother was in estrous, there would be opportunity for a male mating with the mother would also mate with the juvenile. Because of delayed implantation the animal to not give birth until it had reached adult size. This mechanism is an inexpensive way of delaying reproduction without true gestation.

Ermine live solitary lives, and even though territories of both sexes often overlap, rarely encountering other conspecifics except during breeding season (Sandell, 1986; King, 1989). Therefore the possibility of the same male finding and mating with the same female from year to year, and hence inbreeding is unlikely. A male could mate with juvenile females with only a small chance of inbreeding, possibly outweighed by the benefit of increased reproductive output.

The possibility of an adult male harming a juvenile could be reduced by evolving physical and/or behavioral characteristics to act as protection. Behaviorally, the juveniles will give alarm calls, particularly if the adult male is biting hard or rolling around with them. Though the mother does not usually respond to these cries, if they are persistent she will attack the adult male, driving him away from the juvenile. Physically, ermine have an unusual characteristic not found in any other member of their genus. Upon birth they are hairless except for a thick mane of fur on the dorsal side of the neck.

The mane is found in both sexes in the position the male would grab in a mating neckbite, remains the thickest part of the hair for many weeks, and is found only in this species (Hamilton, 1933; Ewer, 1973; King, 1989). It is possible that this mane is linked to neonatal breeding. Ermine mate in a stereotypical position with the male grabbing the partner by the neck with his teeth. If the male is mating with infants, he could damage them if they had bare necks. Therefore the mane could have evolved to protect the juveniles from the males' grasp during matings.

Previous observations have shown that adult males can distinguish between juvenile males and females, dropping the males as soon as they are picked up (DonCarlos *et al.*, 1986; King, 1989). Ewer (1973) and King (1989) speculate that the juveniles' mane contains scent glands which aid the adult male in distinguishing sexes. However, the results of this study show that males do not exhibit discriminatory capabilities. Males do have a shorter MBL for mating attempts with juvenile males, suggesting discrimination of the sexes upon making a mating attempt, though not before, as the number of attempts is as high as or higher than other ermine present.

If male ermine are able to discriminate between sexes, it is curious that they do not commit infanticide (see Hausfater and Hrdy, 1984). Infanticide is almost unknown in this species. Ternovsky (1983) reported only one case where in a litter of 8 the adult male mated with all 4 juvenile females and killed all 4 juvenile males.

Infanticide in other mammals often occurs when an adult male comes upon juvenile conspecifics in which paternity is uncertain, thus ensuring that another male's genes do not proliferate. Usually only juvenile males are killed, as the adult male could mate with the females upon their reaching maturity and therefore promote his genes, though this depends on the species (Packer and Pusey, 1984; Kitchener, 1991). If male ermine can distinguish between sexes, we would expect to see them attempt to kill the males more than females. If there is a strong probability that the male would be the father of the litter, he would likely not kill them. Yet if this were true, he would also not breed with them, because risk of inbreeding would be high. However, infanticide is uncommon in the Carnivora, and is further seen almost exclusively in social species (Packer and Pusey, 1984). Therefore ermine not committing infanticide may be a factor of their solitary social system and not a reproductive strategy.

It seems very cost effective for adult males to mate with young indiscriminately. Solitary living, combined with a high mortality rate, translates into a low chance of inbreeding and of future mating with the same individual. It would therefore seem in the male's best interest to mate with the juveniles, as risks are low and benefits of increased reproductive output high. It also seems to be cost effective for the adult female to allow this behavior, as there is little risk of damage to the young, requiring little expenditure of energy on her part.

Chapter V

CONCLUSIONS

All ontogenetic characteristics of ermine emphasize the rapid development of these animals. Ermine have one of the fastest growth rates of all carnivores (Gittleman & Oftedal, 1987), behaviors and activity patterns change rapidly from week to week during ontogeny, and minimal maternal care is associated with neonatal development. To punctuate this rapidity, neonatal breeding has evolved to possibly hasten sexual maturity and reproductive output. Because of these unusual characteristics, ermine are a fascinating species for a number of issues at the interface of development, behavior, and evolution.

Many questions arise from the present study. The first month after birth was not studied and this could illuminate several of the observed patterns. The frequency of feeding and specific timing of weaning could be determined, as well as further details of nursing: if there is a hierarchy for the nipples (which there likely will not be, based on observations in the present study), if the mother manipulated positioning of the young (maned wolves, *Chrysocyon brachyurus*: Brady and Ditton, 1978; crab-eating foxes, *Dusicyon thous*: Brady, 1978), and if inter-suckling interval relates to the quality or quantity of milk.

Each of the behaviors mentioned in preceding chapters should be studied in more detail, looking at the different types of play, different types of movement, conditions for sleep, etc. An analysis of movement might show that exploratory behaviors increase over ontogeny, especially after separation from the mother. Details of the ontogeny of specific play behaviors might show intersexual differences, such as have been noted in ferrets, where males are greater than females in the frequency of aggressive play behaviors such as neckbite and stand-over (Biben, 1982; Stockman *et al.*, 1986). It would also prove useful to test the hypothesis that sleep increases with activity because the juveniles are more active and therefore require more rest, and whether or not individually housed ermine are indeed differtent in activity patterns from those housed together.

An analysis of 24 hour activity periods is needed for ermine. Other carnivores show a nocturnal pattern (Ewer, 1973) and are less active during the middle of the day (coyote, *Canis latrans*: Ortega, 1988; Andelt and Gipson, 1979; lion, *Panthera leo*: Schaller, 1972; sea otter, *Enhydra lutris*: Ralls and Siniff, 1990). The time of activity can have an effect on lifestyle, such as which prey are available and (in the case of small carnivores who are themselves preyed upon) which predators are a potential threat. Ermine show a more arhythmic pattern, though they are at least partially adapted for a nocturnal lifestyle (King, 1989).

Specific questions need to be addressed concerning social interactions among siblings. Do they have a dominance hierarchy, and if so, does it relate to encounters as adults? Do certain individuals associate more with each other (i.e. play, lie near, etc.), or are associations random? It would be expected that there is little establishment of dominance, as ermine are asocial and do not compete for mates. There would be no requirement for such intraspecific aggression and displays, other than territory maintenance. Similar questions can be asked in relation to the mother's behaviors, such as whether she shows a preference towards a certain individual(s) (it seems from the present study that she does not).

The mother's behaviors obviously need to be studied in more detail. The data presented here suggest that she gives very little direct care. This would make sense, as the rapidly developing young would quickly outgrow a need for much maternal care. However, that is speculative at this point. A more detailed analysis of maternal care could help to assess this hypothesis. A most useful study would be a comparison of maternal care in asocial species with differing growth rates (see Gittleman and Oftedal, 1987). Social species require longer periods of development to acquire skills necessary for group living, and therefore would not be appropriate. Asocial species may not learn such skills, therefore their developmental period should be shorter. Within asocial mammals, the maternal care in those with quicker growth rates should

concentrate on maintenance and ensuring the survival of the young until dispersal, rather than more complicated behaviors such as teaching to hunt.

And of course more research is required for the phenomenon of neonatal breeding. This fascinating event has many implications for the behavior and evolution of ermine, relating directly to reproductive output. Do males have the ability to differentiate between sexes of juveniles? If so, how? Current evidence is conflicting and must be empirically shown one way or another. It seems most likely that they cannot distinguish between sexes, because they can be relatively assured of not being the father of the litter (and therefore will not inbreed), and do not commit infanticide. If it is determined that males do reject juvenile males, an explanation for the lack of infanticide must be given.

It is especially surprising that more work has not been done on ermine because of the ease in caring for them in captivity. They may be housed in relatively small enclosures, are easy and inexpensive to feed, and breed readily in captivity (DonCarlos, personal communication; Feder, personal communication). These animals would make excellent laboratory carnivores for further study.

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APPENDIX

Table A-1. Study behaviors and associated definitions.

Duration variables

Aggression--performing any of the aggressive behaviors as defined by Poole (1966) for polecats (e.g. piloerection, hissing, baring teeth, prostrated and flattened body)

Eat--chew on and consume food item.

Groom self--lick parts of body repeatedly for more than 5 s.

Mouth lick--approach mother and lick her lips and mouth region.

Movement--movement in a given linear direction. Does not include movement such as rolling over or circling a place to lie down.

Non-movement--lying awake but relatively motionless. Includes small movements such as rolling over or circling a place to lie down.

Nurse--suckle mother.

Play--performing any of the play behaviors as defined by Poole (1978) for polecats (e.g. biting, wrestling, open mouth play face)

Sleep--lying motionless with eyes closed for more than 1 m.

Frequency variables

Bite--apply open mouth to an individual. This was not recorded after the juveniles' eyes were open, as it was then determined to be part of play.

Vocalize--making any kind of vocal sound.

Table A-2. Descriptions of observed play behaviors.

Bite--Apply open mouth to an individual. Often an individual would bite another on the mouth.

Chase--One juvenile runs rapidly after another for more than 3 s.

Hop-pounce--Short, low hop onto a sibling, landing with front paws first.

Open-mouth play face--Mouth slightly open, teeth not showing, mouth in slight "O" shape.

Overbear--One individual pounces on or pushes the other so the receiver falls over.

Rear--Juvenile rears up on its hind legs with an open-mouth play face. This can turn into a pounce or simply drop back down into a normal quadripedal position.

Roll/wrestle--Two juveniles roll around while their limbs are intertwined and/or they are biting each other.

Tug-of-war--Two juveniles grab the same object and begin pulling it in opposite directions.

VITA

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