To the Graduate Council:

I am submitting herewith a thesis written by Greta K. Conover entitled "Aspects of Reproductive Behavior in Captive Red Pandas, Ailurus fulgens." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Life Sciences.

J.L. Gittleman, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

ASPECTS OF REPRODUCTIVE BEHAVIOR IN CAPTIVE RED PANDAS, *AILURUS FULGENS*

A thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Greta K. Conover

August 1988

ACKNOWLEDGMENTS

Many people deserve my recognition and gratitude for their assistance to me during the course of this research. A most special thanks goes to Dr John Gittleman who has contributed immeasurable effort, support, criticism, and guidance throughout the study. My committee, Dr. Gordon Burghardt, Dr. Rich Saudargas, and Dr. Michael Pelton, also deserves my gratitude for their consultation and suggestions on numerous occasions. To the "Panda Watch" crew, Patricia, Alicia, Pam, Tracy, Laurie, Melanie, and Cindy - I couldn't have done it without your assistance, gang. And finally, to the members of the Knoxville Zoological Park staff, Dave Eastham, John Croxton, Midgie, Karen and most especially Randy Wolfe, your support of this research and help in all facets of the project made it all possible. Financial support for this research was provided by the University of Tennessee Ethology Program research award and a Science Alliance Upgrade award.

ABSTRACT

Captive populations of red pandas (Ailurus fulgens) are barely replacing themselves and thus there is an immediate need for detailed study of the behaviors involved in reproduction in this species. This study dealt with two aspects of reproduction in red pandas, scent-marking during the breeding period, and maternal care and neonatal development in the nestbound stage. Data were collected at the Knoxville Zoological Park. Three male-female pairs were observed for the scent-marking study. Individuals of both sexes showed significant preferences for scent-marking particular locations, especially prominent points, in each enclosure. Males scent-marked more and in a different fashion than females, although female marking was greater in this study than in previous reports. Females were found to increase marking frequency during the breeding period. However, males were not observed to increase scent-marking, perhaps because outside of breeding male marking behavior was considerably frequent. Certain behavioral features were associated with scent-marking behavior. For example, the number of waddles (defined as each anogenital motion) was positively correlated with duration of scent-marking; and individuals of each sex preferentially sniffed marking areas of the other sex.

A single female red panda and her cub were observed for the maternal care study. In addition, data on three females from the National Zoological Park, Washington, D.C., were analyzed in relation to nest attendance. All females were shown to significantly decrease the amount of time spent in the nest after their cubs' first month of life. Temperature was shown to have no effect on nest attendance. Maternal grooming bouts remained at consistant, low levels through the cub's nestbound stage and this may have facilitated cub defecation. Female-cub resting bouts were found to increase with cub age. In terms of nursing behavior, the amount of time the female spent in the nest had no significant effect on the duration of nursing; nursing periods were frequent and of short duration; and, no teat preference or milk facilitation behavior was exhibited by the cub. Calls between the female and cub seemed to function in establishing contact between the pair and were similar to those reported for raccoons (Procyon lotor). Play behavior was observed in two forms: solitary object play and mother-cub social play; however, both forms occured only in low frequencies. Similar to other carnivores, substantial increases in the rate of cub weight gain were achieved with milk supplements. Cub emergence was observed at 74 days of age. Lengthy

maternal grooming bouts prevented the cub from leaving the nest prior to this.

These results were discussed in relation to the problems generally inherent in captive studies and to the problems specific to this study. Scent-marking and maternal care were further discussed in relation to the solitary social structure and feeding strategy of the red panda. A solitary lifestyle seemed to effect scent-marking behavior in several ways; these included pathway-dominated marking patterns (also characteristic of species feeding on widely dispersed resources such as bamboo), sex-specific olfactory investigation, high frequency marking during breeding, and site-sharing between members of the opposite sex. These factors may enable the marks which are deployed to be more easily intercepted and interpreted; a primary concern for a solitary species such as the red panda.

In conclusion, maternal care and neonatal development in red pandas may be effected by a solitary social system and a folivorous diet. Energetic constraints stemming from a low nutrient diet (bamboo), and a maternally based parental care system were hypothesized to influence slow growth rates in the cub; decreases in maternal nest attendance, and a low incidence of play behavior.

TABLE OF CONTENTS

CHAPTER		PAGE
I.	INTRODUCTION	1
	List of References	6
II.	SCENT-MARKING	10
	Introduction	10
	Methods	14
	Results and Discussion	18
	Site preferences	18
	Sex differences in marking	22
	Changes in scent-marking during breeding	27
	Behavioral correlates of scent marking	30
	Environmental correlates of scent marking	35
	Summary	36
	List of References	38
III.	MATERNAL CARE AND NEONATAL DEVELOPMENT	43
	Introduction	43
	Methods	47
	Results and Discussion	54
	Nest attendance and nest preference	55
	Activities within the nestbox	66
	Nursing	69
	Cub weights	71

Female positions for resting, grooming and nursing..... 73
Vocalizations..... 76
Motor development..... 79
Play..... 79
Carries..... 82
Emergence..... 82
Summary..... 84
List of References..... 86
IV. CONCLUSION..... 93
Problems in Captive Behavioral Research.. 95
Social Structure and Feeding Strategy: Their Effects on Scent-Marking.... 99
Social Structure and Feeding Strategy: Their Effects on Maternal Care and Neonatal Development..... 105
Future Research Goals..... 110
List of References..... 113
VITA..... 119

LIST OF TABLES

TABLE		PAGE
2.1.	Individual Marking Frequencies for each Sex at the Five Sites Most Often Used in Each Enclosure	19
2.2.	Individual Marking Frequencies for the Five Sites Most Often Marked by the Male in Enclosure #3 Prior to Introduction of the Female	21
2.3.	Distribution of Male and Female Marks Comprising Different Number of Waddles	25
2.4.	Comparisons of Marking Frequency Before, During and After Breeding in Enclosure #3	29
3.1.	Female Nest Attendance Summary Statisics for Logged and Unlogged Bout Averages in all Four Enclosures	58
3.2.	Comparisons of Nestbox Use During Two Week Intervals	61

LIST OF FIGURES

FIGURE		PAGE
2.1.	Red Panda Displaying Typical Scent-Marking Posture	13
2.2.	Diagrammatic Representation of Enclosure #3	17
2.3.	Daily Marking Frequencies for Enclosure #3 Male and Female	23
2.4.	Percent of Total Marks Used with Specific Number of Waddles for Males and Females in Enclosure #3	31
3.1.	Diagram of an Example Nestbox Showing Camera Placement for Inside View	48
3.2.	Diagrammatic Representation of Enclosure #1 with Emphasis on Nestbox Placement	51
3.3.	Daily Bout Length Averages for Time Female Spent in the Nestbox Plotted Against Cub Age (Days)	56
3.4.	Regression of Female in Nestbox Bout Averages with Cub Age for KZP Enclosure #1, and NZP Enclosures #A, #98, #1	57
3.5.	Daily Bout Length Averages for Time Female Spent Grooming the Cub Plotted Against Cub Age (Days)	67
3.6.	Duration of Nursing Bouts in Relation to Cub Age (Days)	70
3.7.	Cub Weight Gain as Measured Through the Study	72

CHAPTER I

INTRODUCTION

The reproductive biology of an organism is a composite of physiological, behavioral, and environmental mechanisms all interwoven to produce a complex, yet vitally important aspect to the organism's survival. Reproductive behavior spans the events which begin during courtship and breeding, continue through gestation and culminate with birth and parental care of the neonate. Within the mammalian order Carnivora, the behaviors that characterize each of these stages exhibit extreme interspecific variation, due in part to great diversity in carnivore social organization, feeding strategies, and habitat distribution (Asa 1987; Bekoff et al. 1984; Ewer 1973). Two facets of this complex phenomenon are dealt with in this thesis, scent marking and maternal care during reproduction in captive red pandas, Ailurus fulgens.

Recent comparative reviews have outlined the variation in carnivore scent marking and/or parental care systems as they relate to differences in sociality and resource patterns (Bekoff et al. 1984; Ewer 1973; Gittleman 1985; Macdonald 1980, 1985). While this diversity exists, certain trends can still be followed in scent marking and parental care systems. Maternal

care (in which the female has exclusive responsibility for nourishment and defense of offspring) is the predominant parental care strategy among carnivores as well as most eutherian mammals (Eisenberg 1981). Additionally, while scent marking is attributed with numerous and varied functions (see Chapter II `Introduction'), the function most commonly ascribed is that of signaling reproductive state through increases in marking frequency during courtship (e.g., Gorman 1980; Kleiman 1983; Macdonald 1985; Roberts 1981; Rothman and Mech 1979).

Of course it is the interspecific variation with respect to maternal care and scent marking behavior which allows for hypothesis testing and interpretation of the causal factors involved in these behaviors. The red panda is an excellent species for this kind of study. One reason is that the red panda is unique in being the only folivorous and arboreal member of the order Carnivora (Eisenberg 1981). Comparative studies on folivorous mammals in general have shown them to have decreased metabolic rates, slow postnatal growth, and long periods of parental care (McNab 1980, 1988); these trends also apply to the red panda. Relative to other carnivores, growth rate in body weight of red pandas is slower than any other species (Gittleman and Oftedal 1987). This slow development is reflected in

the extremely long nestbound stage of the young, providing an excellent opportunity for detailed study of mother-cub interactions.

The unique character of red panda scent marking behavior also facilitates study in relation to reproductive behavior. Due to the manner of scent marking in red pandas (a crouch followed by side to side and/or backwards and forwards motions of the hindquarters), it is easy to separate marking behavior from elimination behavior. In other carnivore species, such as canids, marking is primarily through urination, and detailed volumetric measurements must be made to distinguish the two behaviors (Macdonald 1985; Peters and Mech 1975).

It is often difficult to directly observe scent marking and maternal behavior in the field. Therefore, studies performed in zoo settings have become increasingly important in answering specific questions related to reproductive biology (Eisenberg and Kleiman 1977; Gittleman and Conover in press; Hnida 1985; Mertl-Millhollen 1986; Ralls et al. 1987; Rheinhardt 1985; Safar-Herman et al. 1987). Research carried out in captivity may expedite answers to these questions due to opportunities for lab-like manipulations of the animals and environments under scrutiny.

This more-controlled method of study often is

necessary when dealing with the reproductive behavior of endangered species such as the red panda. Due to human infringement upon habitat and its potential effect on breeding success, numbers in the wild may decline to irreversible levels (Roberts and Gittleman 1984; Roberts and Glatston 1988). Recent demographic analyses of the red panda captive population have shown little to no growth; the result of an effective population (that portion consisting of actively breeding members) much smaller than the actual population due to small numbers of breeding animals and suboptimal management practices (Roberts and Glatston 1988). Therefore, captive breeding programs actively involved in research to improve and standardize management practices may be the last chance for this species survival. Popular interest in the giant panda, Ailuropoda melanoluca, has contributed to increased captive research concerning its reproductive biology (e.g. Hodges et al. 1984; Kleiman 1983; Kleiman et al. 1979; Moore et al. 1984; Murata et al. 1986; Schaller et al. 1985). Similar efforts are being directed toward the red panda, the most recent being the creation of the Species Survival Plan, an interzoo breeding network designed to organize worldwide efforts in preservation (Conover and Gittleman 1987; Page 1986). Ideally, this study concerning two aspects of

red panda reproductive biology will contribute to the development of more appropriate and productive management practices so that the numbers of red pandas (in captivity, at least) become more promising.

Chapter Two of this thesis describes scent marking in captive red pandas, primarily in relation to quantitative and qualitative changes which occur during the breeding season. Chapter Three describes the nestbound stage of neonatal development in red pandas; mother-cub interactions and cub behavioral development are detailed. The final chapter is a synthesis of results and conclusions reached in preceding chapters and a discussion of their relation to red panda social structure and feeding strategy.

LIST OF REFERENCES
CHAPTER I

Asa, C.S. 1987. Reproduction in carnivores and ungulates. In: Psychobiology of Reproductive Behavior: an Evolutionary Perspective (Ed. D. Crews), pp. 258-290. Englewood Cliffs, NJ: Prentice Hall.

Bekoff, M., Daniels, T.J., and Gittleman, J.L. 1984. Life history patterns and the comparative social ecology of carnivores. Annu. Rev. Ecol. Syst., 15,191-232.

Conover, G.K., and Gittleman, J.L. 1987. The importance of zoo research in preserving the red panda. Zoo View, 2, 8-10.

Eisenberg, J.F. 1981. The Mammalian Radiations. Chicago: Univ. of Chicago Press.

Eisenberg, J.F., and Kleiman,D.G. 1977. The usefulness of behavior studies in developing captive breeding programms for mammals. Int. Zoo Yb., 17, 81-89.

Ewer, R.F. 1973. The Carnivores. Ithaca, New York: Cornell Univ. Press.

Gittleman J.L. 1985. Functions of communal care in mammals. In: Evolution: Essays in Honour of John Maynard Smith (Eds. P.J. Greenwood, P.H. Harvey, and M. Slatkin), pp. 187-205. Cambridge: Cambridge Univ. Press.

Gittleman J.L., and Conover, G.K. 1988. Mammalian behavior: lessons from captive studies. In: Captive Conservation of Endangered Species: An Interdisciplinary Approach (Eds. J. Demerest, B. Durrant, and E. Gibbons). New York: State University of New York Press.

Gittleman, J.L., and Oftedal, O.T. 1987. Comparative growth and lactation energetics in carnivores. In: Reproductive Energetics in Mammals (Eds A. Loudon and P. Racey), Oxford: Oxford Univ. Press.

Gorman, M.L. 1980. Sweaty mongooses and other smelly carnivores. Symp. Zool. Soc. Lond., 45, 87-105.

Hodges, J.K., Bevan, D.J., Celma, M., Hearn, J.P., Jones, D.M., Kleiman, D.G., Knight, J.A., and Moore, H.D.M. 1984. Aspects of the reproductive endocrinology of the female giant panda (Ailuropoda melanoleuca) in captivity with special

reference to the detection of ovulation and pregnancy. J. Zool. Lond., 203, 253-267.

Hnida, J.A. 1985. Mother-infant and infant-infant interactions in captive sable antelope: evidence for behavioral plasticity in a hider species. Zoo Biol., 4, 339-350.

Kleiman, D.G. 1983. Ethology and reproductuon of captive giant pandas (Ailuropoda melanoleuca). Z. Tierpsychol., 62, 1-46.

Kleiman, D.G., Karesh, W.B., and Chu, P.R. 1979. Behavioural changes associated with oestrus in the giant panda Ailuropoda melanoleuca with comments on female proceptive behaviour. Int. Zoo Yb., 19, 217-223.

McNab, B.K. 1980. Food habits, energetics, and the population biology of mammals. Am. Nat., 116, 106-124.

McNab, B.K. 1988. Rate of metabolism, body size, and food habits in the order Carnivora. In: Carnivore Behavior, Ecology, and Evolution (Ed. J.L. Gittleman), Ithaca, New York: Cornell Univ. Press (in press).

Macdonald, D.W. 1979. Some observations and field experiments on the urine marking behaviour of the red fox, Vulpes vulpes. Z. Tierpsychol., 51, 1-22.

Macdonald, D.W. 1980. Patterns of scent-marking with urine and faeces amongst carnivore communities. Symp. Zool. Soc. Lond., 45, 107-139.

Macdonald, D.W. 1985. The carnivores: order Carnivora. In: Social Odours in Mammals. (Eds. R.E. Brown and D.W. Macdonald), pp. 619-722. Oxford: Clarendon Press.

Mertl-Millhollen, A.S., Goodman, P.A., and Klinghammer, E. 1986. Wolf scent-marking with raised-leg urination. Zoo Biol., 5, 7-20.

Moore, H.D.M., Bush, M., Celma, M., Garcia, A.L., Hartman, T.D., Hearn, J.P., Hodges, J.K., Jones, D.M., Knight, J.A., Monsalve, L., and, Wildt, D.E. 1984. Artificial insemination in the giant panda (Ailuropoda melanoleuca). J. Zool., Lond., 203, 269-278.

Murata, K., Tanioka, M., and Murakami, N. 1986. The relationship between the pattern of urinary oestrogen and behavioural changes in the giant panda. Int. Zoo Yb., 24/25, 274-279.

Page, J. 1986. Close encounters. Zoogoer, 15, 15-19.

Peters, R.P. and Mech, L.D. 1975. Scent-marking in wolves. Am. Scient., 63, 628-637.

Ralls, K., Lundrigan, B., and Kranz, K., 1987. Mother-young relationships in captive ungulates: spacial and temporal patterns. Zoo Biol., 6, 11-20.

Rheinhardt, V. 1985. Courtship behavior among musk-ox males kept in confinement. Zoo Biol., 3, 295-300.

Roberts, M.S. 1981. The reproductive biology of the red panda, Ailurus fulgens, in captivity. Unpublished M.Sc. thesis, University of Maryland.

Roberts, M.S. and Gittleman, J.L. 1984. Ailurus fulgens. Mammalian Species Account No. 222, 1-8.

Roberts, M.S. and Glatson, A.R. 1988. The current status and future prospects of the red panda (Ailurus fulgens) studbook population. Zoo Biol., 7, 47-60.

Rothman, R.J. and Mech, L.D. 1979. Scent-marking in lone wolves and newly formed pairs. Anim. Behav., 27, 750-760.

Safar-Herman, N., Ismail, M.N., Choi, H.S., Mostl, E., and Bamberg, E. 1987. Pregnancy diagnosis in zoo animals by estrogen determination in feces. Zoo Biol., 6, 189-194.

Schaller, G.B., Jinchu, H., Wenshi, P., Jing, Z. 1985. The Giant Pandas of Wolong. Chicago: Univ. of Chicago Press.

CHAPTER II

SCENT-MARKING

Introduction

Carnivores possess a rich repertoire of communication systems. Predominant among these is scent-marking, particularly among solitary species where individuals are spatially and temporally distant from one another. The form and function(s) of scent-marking behavior are diverse across mammalian carnivores (Ewer 1973; Gorman and Trowbridge 1988; Gosling 1982; Macdonald 1985). Seven general functions, all of which may operate in a single species, are attributed to scent-marking:
(1) Identity- Information regarding individual, group or sexual identification is contained in many carnivore odors (e.g. Gorman 1976; Rasa 1973); (2) Status- Information on dominance status, commonly directed to members of the same sex, is contained in the frequency and pattern of marking in many species (e.g., Erlinge et al. 1982; Macdonald 1979). In the context of status function, scent-marking is often associated with visual displays during aggressive encounters; (3) Reproductive Status- Perhaps the most commonly observed function, increases in marking frequency as well as changes in

marking composition and pattern occur during courtship and breeding (e.g. Gorman 1980; Gorman and Trowbridge 1988). Interestingly, even though reproductive function is an important component of scent-marking, no one has tested Darwin's idea (1887) that, among carnivores, an increase in the quality or quantity of a male's odor enhances reproductive success; (4) Spatial Information- The spatial patterns of scent-marking serve as territorial markers (e.g., Kruuk 1978; Peters and Mech 1975; Roper et al. 1986). Although considerable information indicates a circumstantial link between scent-marking and territoriality, most of this evidence does not show that marking deters conspecifics or other potential intruders (Gosling 1982; Macdonald 1985); (5) Temporal Information- Scent-marking reveals when individuals were at a particular location (e.g. Leyhausen and Wolff 1959; Rasa 1973); (6) Foraging- Scent-marking may serve a general book-keeping function by informing an individual of whether it has previously looked for food in a certain local (Henry 1977, 1986; Macdonald 1979); (7) Inter-specific Communication- Several species may mark in the same area, or one species may mark in-between territories of others, to avoid predation (Mech 1977; Stoddart 1979).

In this chapter, data are presented on scent-marking in the red panda, which bear on some of these seven functions. The red panda possesses a number of distinctive traits for a member of the order Carnivora: exclusive dietary preference of bamboo leaves; extremely slow growth rate and behavioral ontogeny (eye opening; den emergence; weaning age); completely furred paws and enlarged radial sessamoid (Gittleman 1988; Gittleman and Oftedal 1987; Roberts 1981; Roberts and Gittleman 1984). Along with these traits also may be included scent-marking: individuals rub ("waddle") their anogenital region in a sideways and/or backwards-and forwards motion (Figure 2.1), a behavior reminiscent of that shown in the giant panda (Kleiman 1983). In addition to the behavioral motion itself, a unique quality of red panda scent-marking is the distinct separation of elimination and scent-marking; unlike many other carnivore species (Kleiman 1966; Macdonald 1985), red pandas urinate and defecate apart from scent-marking. This, however, does not exclude the possibility that urine, feces, integument, or a combination of these components also may serve as scent-marks (Adams 1980). Rather, this characteristic enhances the opportunity to separate specific functions of scent-marking from those associated with general odor secretion, a weakness

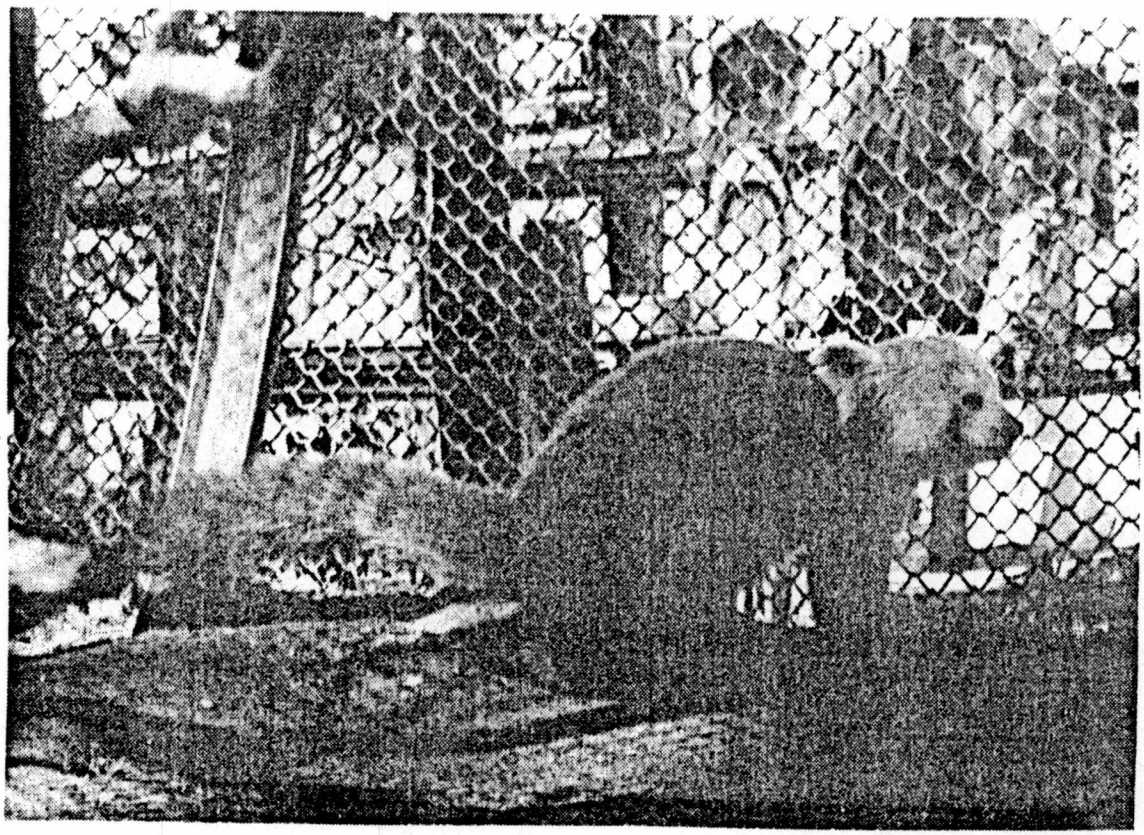


Figure 2.1 Red Panda displaying typical scent-marking posture.

inherent in many studies of carnivore scent-marking (Macdonald 1985).

Previous studies of scent-marking in red pandas include a general ethogram of marking movements and postures (Roberts 1981) and qualitative descriptions of sex differences in marking and related characteristics (Keller 1977). The primary objective in this study was to quantitatively assess differences in the frequency of scent-marking during and outside of the breeding season.

Methods

All scent marking data were gathered at the Knoxville Zoological Park, Knoxville, Tennessee between December, 1986 and April, 1987, a period which included the onset, occurrence and termination of breeding in the red panda. One hundred and twenty nine hours of observation were undertaken over a total of 70 days. Each observation session lasted one to three hours between 1000 and 1500 hours. The time period was selected as one of high activity for the individual animals; it spanned a feeding period which has been previously reported to affect activity levels in red pandas (Roberts 1981, Roberts and Gittleman 1984).

Animals observed in the study were housed in three separate enclosures: each enclosure measuring

approximately ten meters in length, four meters in height, and six meters in width. One enclosure (#2) contained an adult breeding pair; each was eight and a half years of age. Their six month old male cub shared the enclosure with them. Another enclosure (#3) housed a single year and a half old male up until 7 January, 1987 when a newly acquired female of the same age was introduced. She then became an additional subject of the study. The final enclosure (#4) contained an adult breeding pair, a three and a half year old male and an eight and a half year old female. All animals were captive born.

Due to the animals close exposure to public viewers, it was possible to carry out observations within 10 meters of the enclosures. If an animal showed some agitation to the observers' presence, this consistantly subsided within minutes (Jordan and Burghardt 1986) and then observations started. Using check sheets with focal animal sampling, data were systematically collected on the following variables:

Identity of marker - individual performing the scent-marking behavior. Individuals were easily identified within each enclosure by natural facial and body markings.

Time of marking - onset and termination of an individual mark (measured to 1/100 second).

Location of marking - sites used by each individual. Maps of the enclosures allowed identification by number of specific sites (see Figure 2.2). As new sites were adopted, numbers were added to maps.

Number of waddles - the number of motions included when and individual moved its hindquarters in a lateral or ventral direction over an object or ground substrate. For analyses of marking frequency, waddles occuring in rapid succession in either direction were scored as one mark.

Sniffing - scored when an individual placed its nose within a few centimeters of a site before (within one minute), during, or after (within one minute) scent-marking.

Environmental factors - temperature and general climatic conditions (e.g., rain, snow, bright sun) were noted.

General comments - nonsystematic descriptions were made of other events that could be a potential source of individual variability. Entry of keepers, breeding occurrences, presence of viewing public, and general

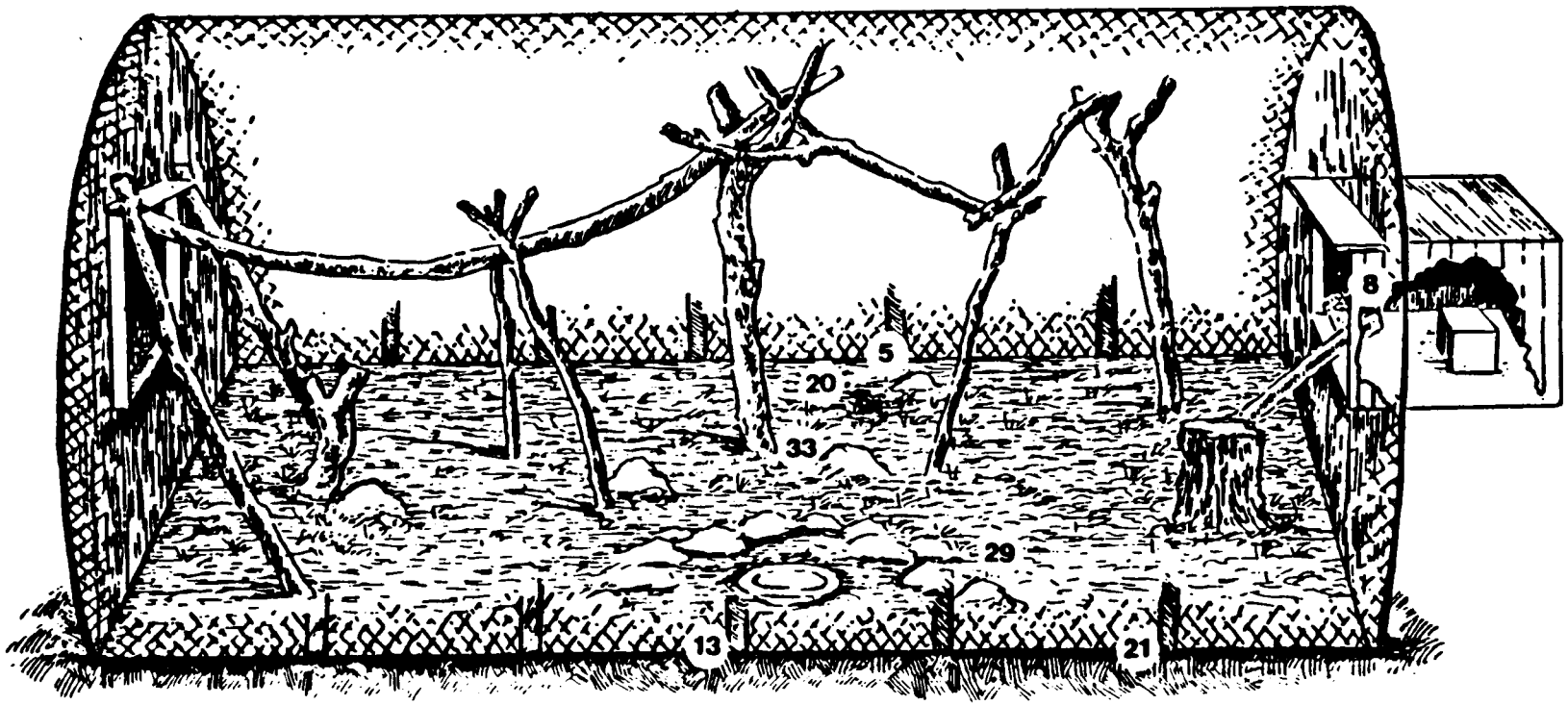


Figure 2.2 Diagrammatic representation of enclosure #3.
Prefered stations are indicated numerically.

changes in animals' state (e.g., sleeping versus awake) are examples of such entries.

Statistical analyses included Chi square, Mann-Whitney U, Analysis of Variance, and Z scores, depending on the appropriateness of assumptions involved with each test (as indicated below). Some data collected from enclosures #2 and #4 were not extensive enough to perform statistical tests, and these are pointed out in the following sections.

Results and discussion

A. Site Preferences:

Both males and females exhibited distinct preferences for particular marking sites (Table 2.1; for numbers of particular mark locations, see Figure 2.2). Of the five most marked sites, significant differences were observed in usage within all enclosures by each sex, except for the male in enclosure #2 (Table 2.1). However, because there was a dramatic difference in marking frequency at the most marked site and the least marked site, a more meaningful analysis was derived from rank-ordering sites in terms of marking frequency and then making pair-wise comparisons between those which rank closest. From the above analysis, four of the six animals significantly preferred two sites; the female also

Table 2.1. Individual marking frequencies for each sex at the five sites most often used in each enclosure.[a]

	Enclosure #2 Site Comparisons							Enclosure #3 Site Comparisons							Enclosure #4 Site Comparisons						
	Site	Freq.	9	6	10	13	7	Site	Freq.	33	5	20	29	8	Site	Freq.	13	16	14	10	2
FEMALES	9	25	-	3.8	4.6*	6.4*	4.3**	33	106	-	17.7***	58.7***	64.4***	78.7***	13	14	-	7.1**	7.1**	7.1**	9.0**
	6	13			0.1	0.4	0.7	5	53		-	14.9***	18.5***	24.2***	16	3		-	0.0	0.0	0.2
	10	12			-	0.2	0.4	20	20			-	0.2	1.5	14	3			-	0.0	0.2
	13	10				-	0.1	29	17				-	0.5	10	3				-	0.2
	7	9					-	8	13					-	2	2					-
	Site	Freq.	12	9	6	10	19	Site	Freq.	33	5	13	8	21	Site	Freq.	4	7	3	9	10
MALES	12	13						33	147	-	0.7	21.2***	27.3***	29.9***	4	200	-	125.6***	129.7***	156***	166.7***
	9	10	Overall variation					5	133		-	14.3***	19.5***	21.8***	7	30		-	0.1	4.3*	7.7**
	6	7	not significant					13	78			-	0.1	0.8	3	28			-	3.3	6.4*
	10	6						8	70				-	0.1	9	16				-	0.3
	19	4						21	67					-	10	12					-

[a]Levels of significance are as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

preferred these sites, though one was selected over the other. Also, following introduction of the female into the enclosure, the male in #3 changed from displaying no preference (Table 2.2) to exhibiting a clear preference (as in Table 2.1). In general, all locations of marking sites were comprised of prominent points in the enclosures (see Figure 2.2).

Discussion:

Previous studies of scent-marking behavior generally have agreed on two inherent characteristics of preferred marking sites, placement on main travel routes and prominance of target objects (Macdonald 1985; Moran and Sorensen 1986; Stoddart 1980). Keller (1977) discussed various travel pathways which pandas used; the "main circuit" encompassed those marking sites most frequently used. Main travel circuits in all enclosures were found to connect important areas such as sleeping sites and foraging stations. Results in this study parallel these findings by revealing that several of the preferred sites were near water and food sources (see locations #8, #13 in Figure 2.2), latrines (#20,#5), and a denning area (#8). All of the marked sites, both statistically preferred and not, were prominent objects within the enclosures (e.g., rocks; knots on logs; metal protrusions in the enclosure); this supports the idea that marking sites are landmarks

Table 2.2. Individual marking frequencies for the five sites most often marked by the male in enclosure #3 prior to introduction of the female.[a]

Site	Mark Frequency
12	42
3	43
19	30
6	26
1	25

[a]No statistical difference was shown for site preference ($X^2 = 4.23$, NS).

which provide a means of orientation for the marking animal. Prominent sites also may facilitate communal use of the marking area by communicating certain kinds of information (e.g. reproductive cycle; aggressive states) more visibly and/or olfactorily.

B. Sex Differences in Marking:

Significant differences in scent-marking were observed beween males and females. The male in enclosure #3 showed consistantly higher marking frequency than the female ($t = 4.06$, $n = 1,519$; $p < 0.001$; Figure 2.3). Observations on scent-marking for each sex in the other two enclosures were not of suitable sample size to perform statistical comparisons. Similar trends, however, were shown by the male and female in enclosure #4 with marking rates 14m/hr and 2m/hr, respectively. By contrast, in enclosure #2 the female exhibited a marking rate of 12 m/hr and the male 2m/hr.

In addition to the quantitative difference in scent-marking between the male and female in enclosure #3, a qualitative difference also was observed among animals in all enclosures. Detailed data were collected on the direction of hindquarter movement while scent-marking for each sex. All males displayed two movement patterns: a back-and-forth motion and a

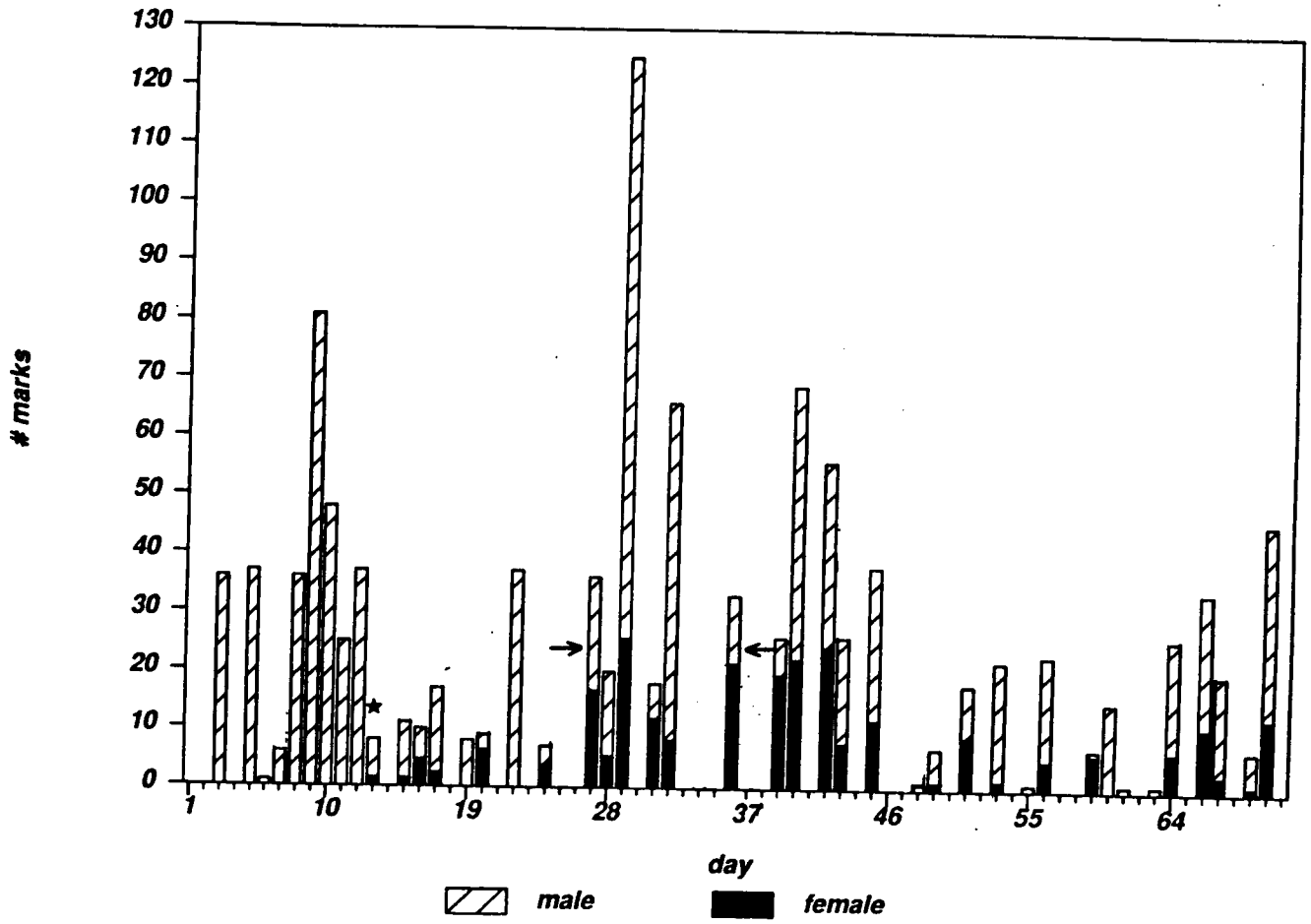


Figure 2.3 Daily marking frequencies for enclosure #3 male and female. Arrows indicate onset and termination of breeding. Male mark frequency: x = 23.6, s = 24.8. Female mark frequency: x = 6.40, s = 7.61. (*) indicates day female introduced into the enclosure.

side-to-side motion. Male marks comprising unidirectional movement occurred in 41% cases; 59% were bidirectional marks (n = 157). In contrast, females only marked in a lateral fashion (n = 80).

Given the dimorphism in mark direction, the difference in the number of waddles for males and female was examined. Pooling the data resulted in a statistical difference for each sex in number of waddles (males = 1,337; females = 468; $X^2 = 13.2$; $p < 0.05$). However, this was due to an extremely large sample size. A more accurate analysis is to test for sex differences with each waddle number. This test found both males and females exhibit similar patterns in the number of waddles per mark (Table 2.3). Additional analyses of the number of waddles used on individual sites showed no correlation between waddle number and site used for either males ($r = 0.039$, $n = 533$), or females ($r = -0.108$, $n = 307$).

Discussion:

The tendency for male red pandas to exhibit higher marking frequencies than females coincides with sex-related trends observed in other mammals (Stoddart 1980; Macdonald 1985; Gorman and Trowbridge 1988). Keller (1977) measured mark frequencies in one captive red panda group and reported marking frequencies in males ten times greater than in females. The present

Table 2.3. Distribution of male and female marks comprising different number of waddles.[a]

Waddle #	%Male marks	% Female marks	Z score
1	15	12	0.83
2	41	40	0.21
3	18	20	-0.35
4	14	19	-1.31
5	5	5	0.12
>5	7	4	0.96

[a]Z scores reflect pairwise comparisons between males and females; significant differences were not observed in any case.

study showed a less marked difference: male marking frequencies averaged six times higher than females. This may be partially explained by the difference in composition of captive individuals in the two studies. Keller's population included multiple female groups (housed with a single male), consequently, a hierachical effect was observed in marking behavior: females marked less as their "rank" declined. Thus, on average, females living in a hierarchy may show suppressed marking frequencies compared to those living singly or alone with a male, as represented in this study group. The female which exhibited an opposite trend (higher marking frequency than the male) may have been affected by the presence of her six month old cub. Red panda females with cubs show elevated levels of activity which would tend to increase the likelihood of marking behavior. Also, when young are initially exploring their environment immediately following nest emergence, protective females may show an increase in marking (Gittleman, pers. comm.).

The highest level of marking was found in enclosure #3. Many factors were probably involved, but a primary one might have been the introduction of an unfamiliar female. Several studies have shown an increase in marking activity during initial encounters of a pair (e.g., Speothos venaticus, bushdog: Porton

1983; Canis lupus, wolf: Rothman and Mech 1979). Establishment and mutual acceptance of pair bonds may require higher rates of olfactory communication, especially in species with reduced visual acuity, to facilitate interaction between members of the pair (Porton 1983). Aggression between the introduced female and the male also may be a contributing factor. Considerable evidence suggests a high correlation between motivation towards aggression and increased rates of marking behavior (see Biben 1982; Gosling 1982; Rasa 1973). For example, in genets (Genetta genetta), increased rates of ano-urogenital marking, flank and hindleg rubbing were found during aggressive encounters with unfamiliar females (Roeder 1983). The similarity with the findings of this study may have contributed to the higher rates of marking behavior in enclosure #3 when compared to the other two enclosures.

C. Changes in Scent-Marking During Breeding:

As in the previous analysis, only data gathered from enclosure #3 were sufficient to perform statistical analyses on the changes of marking during breeding periods. Scent-marking frequencies before, during and after breeding of the male and female were compared (Figure 2.3). The female marked significantly more during breeding than outside of the season (Table

2.4). The male, however, showed no significant change with the onset of breeding.

Discussion:

Generally, increased scent-marking in females of other carnivore species has been observed during breeding (e.g., Herpestes auropunctatus, Indian mongoose: Gorman 1980; Genetta tigrina, large spotted genet: Wemmer 1977) or during the birthing season (e.g., Helogale undulata rufula, African dwarf mongoose: Rasa 1973). This trend also agrees with observation on the giant panda (Ailuropoda melanoleuca), where both sexes increase their marking frequency during mating, although males mark more than females (Kleiman 1983). It is likely that in this study males did not reflect a significant increase in marking during estrous because frequency of male marking was high even outside of the breeding season.

The primary functional explanation for increased marking during reproduction is that, in natural populations of solitary carnivores where individuals of each sex maintain territories outside of breeding, scent-marking communicates breeding receptivity (see Gorman and Trowbridge 1988; Macdonald 1985). Field data on home range movements and boundaries of red pandas in natural populations indicate that individuals of each sex maintain solitary activities outside of the

Table 2.4. Comparisons of marking frequency before, during, and after breeding in enclosure #3.

Male marks/hour	U value	Female marks/hour	U value
Before/During		Before/During	
n = 716	49.5, NS	n = 104	8.5, $p<0.01$
During/After		During/After	
n = 838	48.5, NS	n = 220	27.0, $p<0.01$

breeding season (Johnson et al. in press; Schaller et al. 1985). Certainly, the results presented here on captive animals are consistent with this explanation. Nevertheless, as with other behavior patterns which are frequently provoked and influenced by artificial surroundings, the total variation of scent-marking in red pandas may be attributable to various non-reproductive factors.

D. Behavioral Correlates of Scent-Marking:

Duration of waddling and marking - On two separate occasions the duration of both male and female scent-marks were timed to 1/100 second. For each timed mark the number of waddles was noted. The correlation beween duration of scent-marking and number of waddles was significant ($r = 0.90$, $n = 64$; $p < 0.05$). Thus, it was concluded that number of waddles is indicative of mark duration. The number of waddles per mark ranged from 1-17, with average number of waddles per mark being two (Figure 2.4).

Discussion:

With the behavioral motion of waddling (see definitions of `Variables') comprising the beginning and termination of scent-marking, it is hardly surprising that waddle number and duration of scent-mark are correlated. Indeed, in other species

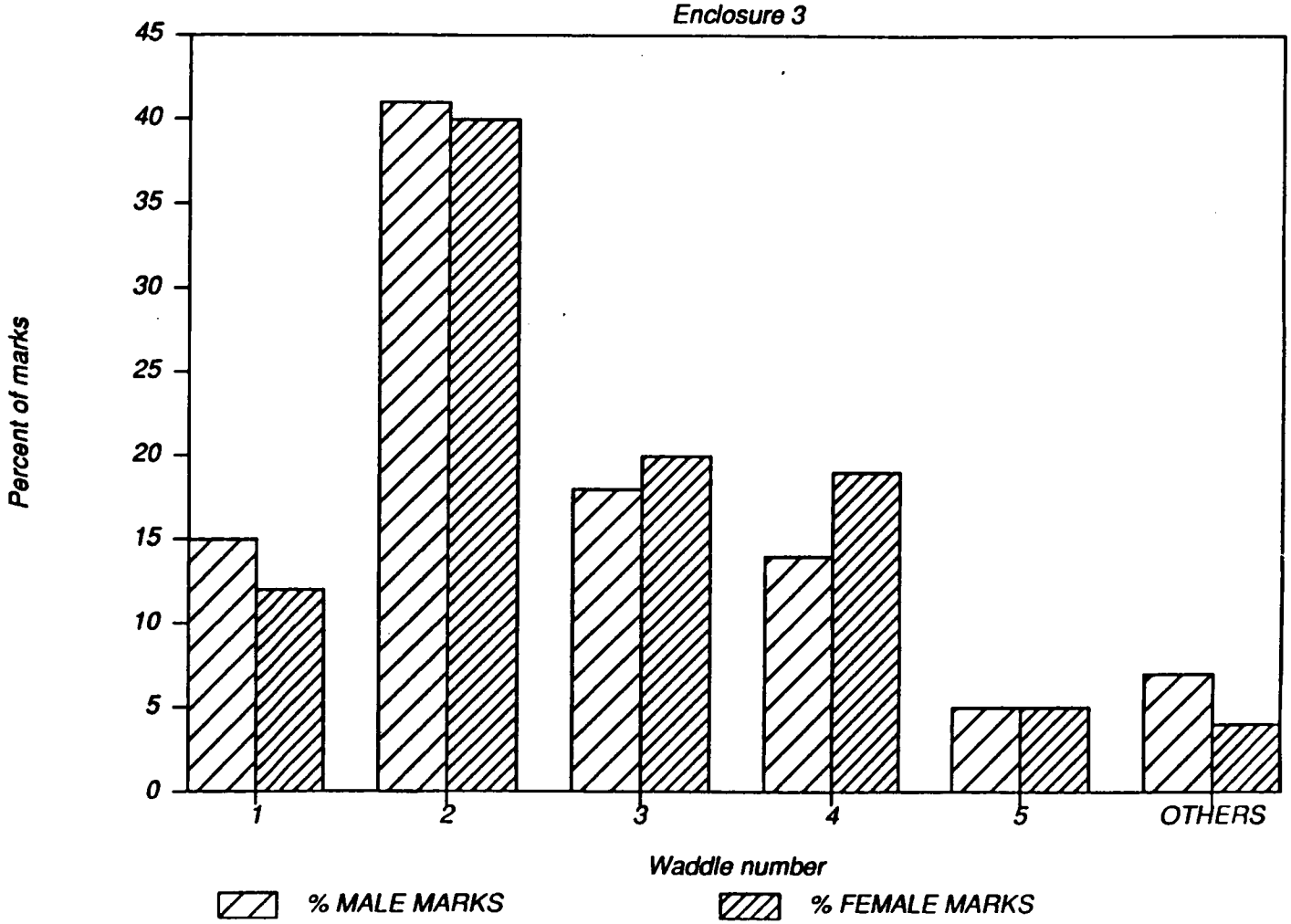


Figure 2.4 Percent of total marks used with specific number of waddles for males and females in enclosure #3.

where mark-specific behaviors contribute to scent-marking, similar correlations were observed. For example, in snow leopards (Panthera uncia) individuals scrape and tred with their hind feet (termed "scuffing") while marking. The number of scuffs is positively correlated with duration of marking, even with marking duration ranging from 1-47 seconds and individual leg movements ranging from 2-60 (Wemmer and Scow 1977). If number of waddles reflects intensity or variability in the kind of mark, it would be interesting to analyze the chemical content of marks of different waddle number. With the male expressing a different type of waddle movement, which may relate to the unusually forward location of the penis (or glandular region around it) from the anus (Flower 1870; Roberts and Gittleman 1984), these may lay down scents of different chemical composition specific to male-female attractant.

Sniffing and marking - As sniffing or other investigatory behaviors often are associated with scent-marking in mammals (Eisenberg and Kleiman 1972; Ralls 1971), this relationship was investigated. To account for individual differences in activity levels which may influence the incidence of sniffing, the daily number of sniffs performed by each individual was divided by that individuals' marking frequency. No

difference was observed in sniffing or other investigatory behaviors between males and females (enclosure #2: U = 48.5, n = 18; n.s.; #4: U = 14.5, n = 14; n.s; #3: Z = -0.525, n = 66; n.s).

Sniffing particular sites did not occur randomly for either males or females. Z scores were computed utilizing data from enclosure #3 to determine the probability of the following situations:

a) male sniffs a site previously marked by female ($z = 4.17$).

b) female sniffs a site previously marked by male ($z = 3.48$).

c) male sniffs a site previously marked by himself ($z = -3.48$).

d) female sniffs a site previously marked by herself ($z = -4.17$).

All levels of significance were $p < 0.001$. Thus, there was a significant probability of the first two situations occuring more frequently than expected. Sniffing one's own mark was, however, less likely.

Discussion:

Communication through olfaction is clearly a predominant feature of scent-marking and consequently sniffing is closely linked with mammalian scent-marking behaviors. This observation has been justified for many carnivores (e.g., Suricatta suricata, meerkat:

Moran and Sorensen 1986; Procyon lotor, raccoon: Ough 1982; African dwarf mongoose: Rasa 1973; large spotted genet: Wemmer 1977; Panthera uncia, snow leopard: Wemmer and Scow 1977), whereby individuals sniff before and after scent-marking. These results indicate that both sexes preferentially sniff marked sites in a sex-related fashion, a finding inconsistant with Roberts' (1981) claim that females "rarely turn to visually or olfactorily examine scent-marks" (p.142). Sex-specific olfaction indirectly suggests that scent-marking cues may be directed to individuals of the other sex. Other studies of carnivores report mixed results on the abilities of one sex to discriminate another. In some species, particularly those residing in groups, individuals are capable of discriminating between sexes and group members (Herpestes auropunctatus, small Indian mongoose: Gorman 1976; Meles meles, European badger: Kruuk et al. 1984; Hyaena brunnea, brown hyena: Mills et al. 1980; African dwarf mongoose: Rasa 1973). By contrast, among primarily solitary carnivores, individuals of one sex may preferentially select the odors of the other sex (Erlinge et al. 1982; Powell 1979). Obviously, the results presented here do not directly test this idea because comparisons were not made between an individual of one sex and the other sex. Nevertheless, the

observations of red panda sniffing indicate that preferences do occur in relation to the sex depositing a particular scent-mark.

E. Environmental Correlates of Scent-Marking:

Regression analyses were performed on daily temperatures and marking frequency in enclosure #3. Temperatures ranged from -1 to 24°C for the duration of the study. For the male and female, there appeared to be no association between temperature and marking frequency ($r = 0.078$ and $r = 0.058$, respectively). Low marking frequencies in enclosures #2 and #4 did not warrant statistical examination.

Discussion:

Climatic factors are well-known to affect the activity cycles of captive mammals which, in turn, might influence scent-marking patterns. For example, in captive dwarf mongooses, cold, cloudy, or rainy weather produced significant declines in scent-marking (Rasa 1973). General activity rhythm was not continuously monitored during the observation periods when scent-marking was recorded. Nevertheless, in a similar behavioral study of red pandas at the National Zoological Park (Gittleman 1988), the percentage of active time (defined by eating, drinking, walking or playing) in a given sampling period did not correlate

with incidence of scent-marking ($r = 0.163$, $n = 145$; n.s.), even though activity was influenced by temperature ($r = 0.193$, $n = 185$; $p < 0.05$; temperature defined as average daytime value). Nevertheless, at a certain level scent-marking must be associated with activity because an individual cannot mark unless it is active and moving.

Summary

1. Individuals of both sexes showed significant preferences for scent-marking particular locations, especially prominent points, in each enclosure. These locations might serve as effective territorial signposts.

2. Males scent-marked more and in a different fashion than females, although female marking was greater in this study than in previous reports. Frequency of scent-marking may relate to general composition of animals (length of exposure together, presence of offspring) and hierarchical relationships among individuals.

3. Females increase marking frequency during the breeding period. Males were not observed to increase scent-marking, perhaps because outside of breeding male marking behavior was already at an elevated level.

4. Certain behavioral features are associated

with scent-marking behavior. Number of waddles (defined as each anogenital motion) is positively correlated with duration of scent-marking, which may correspond to the strength or information conveyed by a particular mark. Individuals of each sex preferentially sniff marking areas of the other sex. Sniffing before and/or after scent deposition is commonly observed in other carnivores and thought to emphasize the important communicative function of scent-marking.

LIST OF REFERENCES
CHAPTER II

Adams, M.G. 1980. Odour-producing organs of mammals. Symp. Zool. Soc. Lond., 45, 57-86.

Biben, M. 1982. Urine-marking during agonistic encounters in the bush dog (Speothos venaticus). Zoo Biol. 6, 359-362.

Darwin, C. 1887. The Descent of Man and Selection in Relation to Sex. London: Murray.

Eisenberg, J.F., Kleiman, D.G. 1972. Olfactory communication in mammals. Ann. Rev. Ecol. Syst. 3, 1-32.

Erlinge, S., Sandell, M., and Brinck, C. 1982. Scent-marking and its territorial significance in stoats, Mustela erminea. Anim. Behav., 30, 811-818.

Ewer, R.F. 1973. The Carnivores. Ithaca, New York: Cornell Univ. Press.

Flower, W.H. 1870. On the anatomy of Ailurus fulgens. Proc. Zool. Soc. Lond., 1870, 752-769.

Gittleman, J.L. 1988. The behavioral energetics of lactation in a herbivorous carnivore, the red panda (Ailurus fulgens). Ethology, (in press).

Gittleman, J.L. and Oftedal, O.T. 1987. Comparative growth and lactation energetics in carnivores. In: Reproductive Energetics in Mammals (Eds. A. Louden and P. Racey), pp. 41-77. Oxford: Oxford Univ. Press.

Gorman, M.L. 1976. A mechanism for individual recognition by odour in Herpestes auropunctatus (Carnivora: Viverridae). Anim. Behav., 24, 141-145.

Gorman, M.L. 1980. Sweaty mongooses and other smelly carnivores. Symp. Zool. Soc. Lond., 45, 87-105.

Gorman, M.L. and Trowbridge, B.J. 1988. The role of odor in the social lives of carnivores. In: Carnivore Behavior, Ecology, and Evolution. (Ed. J.L. Gittleman), Ithaca: Cornell Univ. Press.

Gosling, L.M. 1982. A reassessment of the function of scent-marking territories. Z. Tierpsychol., 60, 89-118.

Henry, J.D. 1977. The use of urine marking in the scavenging behaviour of the red fox (Vulpes vulpes). Behaviour, 61, 82-105.

Henry, J.D. 1986. Red Fox, the Catlike Canine. Washington, D.C.: Smithsonian Institution Press.

Johnson, K.G., Schaller, G.B., and Jinchu, H. (in press). Comparative behavior of red and giant pandas in the Wolong Reserve, China. J. Mammal.

Jordan, R.H. and Burghardt, G.M. 1986. Employing an ethogram to detect reactivity of black bears (Ursus americanus) to the presence of humans. Ethology, 73, 89-115.

Keller, R. 1977. Beitrag zur ethologie des kleinen Pandas (Ailurus fulgens, Cuvier, 1825). Unpublished Ph D. dissertation, University of Zurich, Switzerland.

Kleiman, D.G. 1966. Scent-marking in the Canidae. Symp. Zool. Soc. Lond., 18, 167-177.

Kleiman, D.G. 1983. Ethology and reproduction of captive giant pandas (Ailuropoda melanoleuca). Z. Tierpsychol., 62, 1-46.

Kruuk, H. 1978. Spatial organization and territorial behaviour of the European badger Meles meles. J. Zool., 184, 1-19.

Kruuk, H., Gorman, M., and, Leitch, A. 1984. Scent-marking with the subcaudal gland by the European badger, Meles meles. Anim. Behav., 32, 899-907.

Leyhausen, P. and Wolff, R. 1959. Das Revier einer Hauskatz. Z. Tierpsychol., 16, 666-670.

Macdonald, D.W. 1979. Some observations and field experiments on the urine marking behaviour of the red fox, Vulpes vulpes. Z. Tierpsychol., 51, 1-22.

Macdonald, D.W. 1985. The carnivores: order Carnivora. In: Social Odours in Mammals (Eds. R.E. Brown and D.W. Macdonald), pp.619-722. Oxford: Clarendon Press.

Mech, L.D. 1977. Wolf-pack buffer zones as prey reservoires. Science, 198, 320-321.

Mills, M.G.L., Gorman, M.L., and, Mills, M.E.J. 1980. Scent-marking behavior of the brown hyaena Hyaena brunnea. S. Afr. J. Zool., 15, 240-248.

Moran, G. and Sorensen, L. 1986. Scent-marking behavior in a captive group of meerkats (Suricatta suricata). J. Mammal., 67, 120-132.

Ough, W.G. 1982. Scent-marking of captive raccoons. J. Mammal., 63, 318-319.

Peters, R.P. and Mech, L.D. 1975. Scent-marking in wolves. Am. Scient., 63, 628-637.

Porton, I. 1983. Bush dog urine-marking: its role in pair formation and maintenance. Anim. Behav., 31, 1061-1069.

Powell, R.A. 1979. Mustelid spacing patterns: variations on a theme by Mustela. Z. Tierpsychol., 50, 153-165.

Ralls, K. 1971. Mammalian scent-marking. Science, 171, 443-449.

Rasa, O.A.E. 1973. Marking behaviour and its significance in the African dwarf mongoose, Helogale undulata rufula. Z. Tierpsychol., 32, 449-488.

Roberts, M.S. 1981. The reproductive biology of the red panda, Ailurus fulgens, in captivity. Unpublished M.Sc. thesis, University of Maryland.

Roberts, M.S. and Gittleman, J.L. 1984. Ailurus fulgens. Mammalian Species Account No. 222, 1-8.

Roeder, J.J. 1983. Etude des interactions sociales entie male et femelle chez la genette (Genetta genetta L.): Relations entre marquage olfactif et agression. Z. Tierpsychol., 61, 293-310.

Roper, T.J., Shepherdson, G.J., and, Davis, J.M. 1986. Scent-marking with faeces and anal secretion in the European Badger (Meles meles: seasonal and spatial characteristics of latrine use in relation to territoriality. Behaviour, 97, 94-117.

Rothman, R.J. and Mech, L.D. 1979. Scent-marking in lone wolves and newly formed pairs. Anim. Behav., 97, 94-117.

Schaller, G.B, Jinchu, H., Wenshi, P., and, Jing, Z. 1985. The Giant Pandas of Wolong. Chicago: Univ. of Chicago Press.

Stoddart, D.M. 1979. Some responses of a free living community of rodents to the odors of predators. In: Chemical Signals (Eds. D. Muller-Schwarze and R.M. Silverstein), pp. 1-10. London: Plenum Press.

Stoddart, D.M. 1980. The Ecology of Vertebrate Olfaction. London: Chapman and Hall.

Wemmer, C.M. 1977. Comparative ethology of the large-spotted genet (Genetta tigrina) and some related viverrids. Smithsonian Contributions to Zoology, 239, 1-93.

Wemmer, C.M. and Scow, K. 1977. Communication in the Felidae with emphasis on scent-marking in contact patterns. In: How Animals Communicate (Ed. T.A. Sebeok), pp.749-766. Bloomington: Indiana Univ. Press.

CHAPTER III

MATERNAL CARE AND NEONATAL DEVELOPMENT

Introduction

Possession of mammary glands and their use in providing nourishment to neonatal young is a characteristic which unifies the Class Mammalia (Eisenberg 1981; Pond 1977). As a result of variation in several parameters of lactation (e.g. milk composition, milk production), the mother-infant relationship is extremely complex and profoundly influences many aspects of neonatal growth as well as modes of parental care. As typically explained in terms of parental investment theory (Maynard Smith 1977; Trivers 1972), most mammals display strictly maternal care (approximately 50%: Eisenberg 1981). This trend also applies to the order Carnivora, even though communal and biparental forms are also found (Gittleman 1985a, 1988a; Kleiman and Malcolm 1981).

The length and form of maternal care in carnivores are extremely varied. This behavioral variation is thought to reflect phylogenetic constraints and ecological differences in the demands of the young at different stages of development (Ewer 1973; Kleiman and Eisenberg 1973).

One form of maternal care is expressed by the cheetah (Acinonyx jubatus). The female of this species plays a very active maternal role while raising her young (Eaton 1974). General observations of cheetah maternal care show that in the first six months after birth the mother provides all nourishment to an average of four cubs. The following six months are spent teaching the cubs necessary skills for hunting while at the same time providing most of their food from kills. Analysis of predatory success during this period has shown a drop in the mother's rate of hunting success due to the cubs' inexperience in stalking (Caro 1987), thus underscoring the potential cost of a lengthy, active maternal role. Although after approximately 12 months the cubs are effective hunters in their own right, female cheetahs remain with their cubs and hunt with them for up to two years.

By contrast, the mother-young association in least weasels (Mustela nivalis), is of much shorter duration. By three weeks of age the young are able to consume solid food (e.g., mice) provided by the female. Six week old weasels can successfully kill their own prey. It has been shown experimentally that the age at which this hunting success occurs seems to be uneffected by the presence or absence of the female. Weaning is complete and the young disperse at

approximately seven weeks (Heidt 1970). Thus a less interactive, ephemeral maternal role is being displayed by the least weasel than by the cheetah.

The causal factors involved in these interspecific variations are not often readily apparent. The complexity of the problem is fully understood with the realization that maternal care is based on a parent-offspring relationship (Rheingold 1963), a relationship which may change causally from birth to weaning (Rosenblatt 1976). How the offspring reacts to or affects the mother's behavior is just as crucial to understand as is the mother's role (Ewer 1973; Harper 1981; Hofer 1981). Recent comparative studies have outlined some of the factors involved with variation in parental care strategy among carnivores. For example, the method of parental care influences maternal effort (as reflected by litter growth rates). Species with maternal care exhibit slower growth rates relative to those species in which care is biparental or communal (Gittleman and Oftedal 1987). How variability involved within one type of parental care strategy (e.g., maternal care as described above) is manifested on measurable traits such as litter growth or the inherent behavioral variation is an area still in need of scrutiny. This would necessarily require more detail in studies examining maternal care systems.

Field studies of carnivores generally are not helpful for showing detailed behaviors during the care giving period, due to most carnivores giving birth in well protected (and therefore inaccessible for field study) areas such as dens, burrows, or hollow logs. Thus, captive studies can be of great value in determining the specifics of mother-infant interaction necessary for analysis of this kind. Captive studies can provide, in a sense, entrance into the natal nest through the use of cameras or plexiglass observation windows that allow behavior within to be recorded. Most of the information we have gained on carnivore mother-infant interaction has been provided by captive studies (e.g., Canidae: Biben 1983; Mertl-Millhollen et al. 1986; Ryon 1986; Ursidae: Burghardt and Burghardt 1972; Peking Zoo 1974 in Kleiman 1983; Procyonidae: Montgomery 1969; Roberts 1981; Seiber 1986; Felidae: Adamson 1969; Barrett and Bateson 1978; Mendl 1988; Viveridae: Ewer 1973; Wemmer 1977; for review, see Bekoff 1988).

The unusually long nestbound period of the red panda provides an excellent opportunity for analyzing behaviors associated with prolonged maternal care. Information concerning the nestbound stage of the red panda has primarily centered around physical development of the cubs (Gray 1970; Roberts 1975). The

purpose of this study was to document for the first time activities taking place within the nestbox from birth to the time of nest emergence in young. Mother-cub interactions and the cub's behavioral development will primarily be discussed in relation to ecological factors such as diet, which have been shown to influence maternal effort (Gittleman and Oftedal 1987).

Methods

Data concerning maternal care and behavioral development in captive red pandas were collected at the Knoxville Zoological Park (KZP) between 24 June, and 29 September, 1987. This period includes birth to nest emergence of the young. A total of four hundred and twenty eight hours of observation were performed. Observation sessions lasted from three to nine hours between 0800 and 1700 hours. Prior to parturition, two enclosures (#1 and #2, configurations detailed in Chapter II `Methods' section) were equipped with a total of eight Magnavox observation cameras (model # MC3411-AL01), four per enclosure. One camera viewed the entire enclosure, the other three were placed inside nest boxes or denning areas so that cubs could be constantly viewed (see Fig. 3.1). An area within the nestbox of approximately 10 centimeters on each

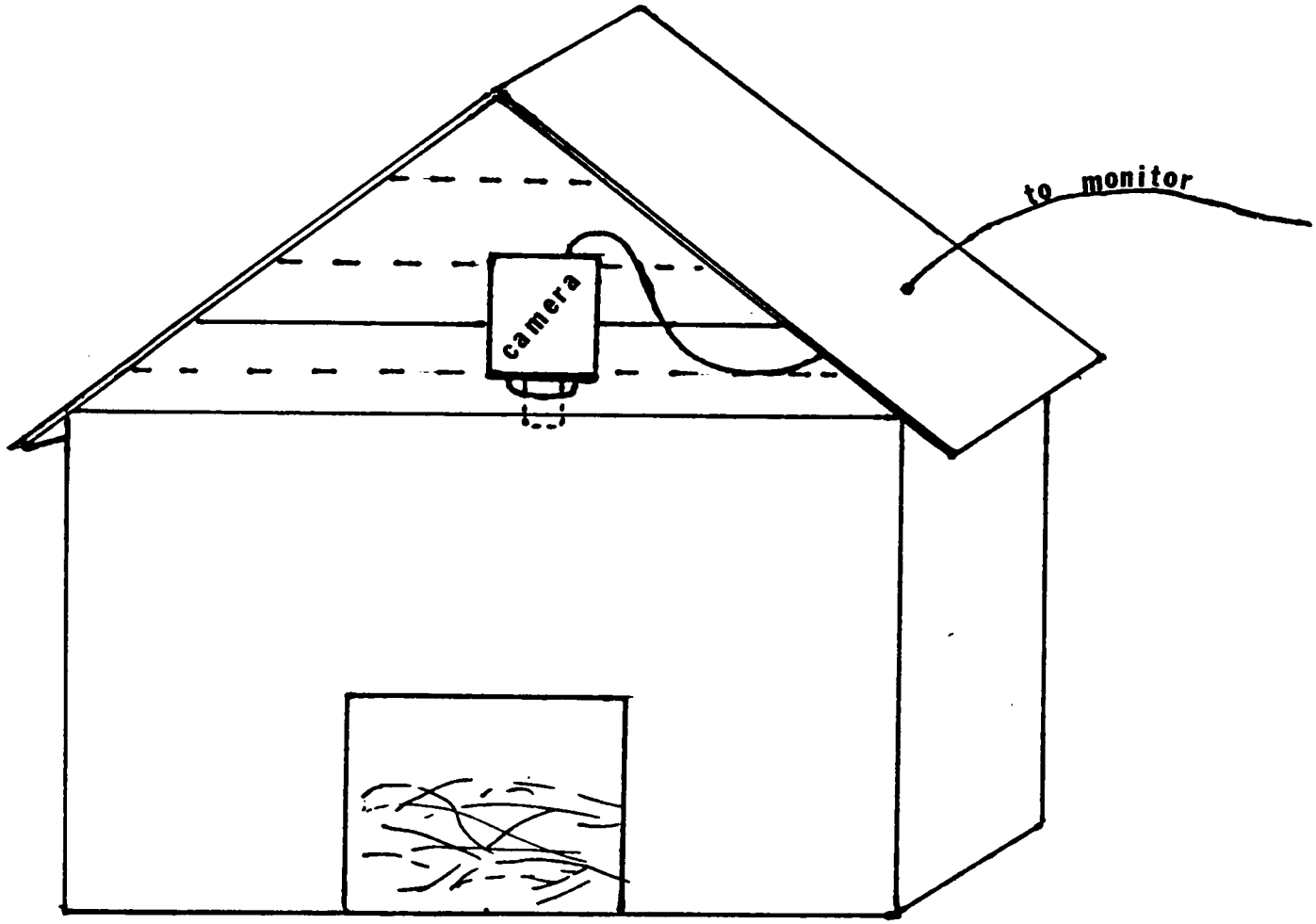


Figure 3.1 Diagram of an example nestbox showing camera placement for inside view.

side was, however, not in view at any time due to focal limitations of the wide angle lens. This at times created situations when the cub was "off screen" and therefore not under observation. Three Magnavox monitors (model# MC3510-AL01) allowed view of the nestboxes from a building located approximately 200 meters from the panda enclosures. Noteworthy behaviors could be recorded using a Magnavox VCR (model# VR9520AT01). Continuous tape recording was not attempted due to lengthy sleeping bouts by the cub or periods in which she was entirely out of view, though these periods were recorded on check sheets. Enclosures utilized for the study were:

Enclosure #1 - consisted of a six year old female (Kelly) and a seven year old male (Rodney). This pair had previously sired two litters at KZP, one in 1983 (the year the male was introduced), the other in 1984.

Enclosure #2 - consisted of a male-female pair (Dave and Dierdra) each eight years of age. This pair had previously sired five litters at KZP spanning breeding seasons from 1981 to 1986.

Two cubs were born to the female in enclosure #2 on 30 July, 1987. They were subsequently removed after two days due to a severe decrease in their body weight. One of the cubs (sex unknown) died within a few hours,

while the littermate (a female) survived and was successfully handraised. The female in Enclosure #1 gave birth to a single female cub on 24 June, 1987. The cub was observed from birth to the age of 97 days after it was determined the cub was consistantly leaving the nestbox on its own. Three nestboxes were used by the female in enclosure #1 throughout the study. Nestbox #1 was located inside an enclosed den, nestboxes #2 and #3 were outside in the enclosure (Fig. 3.2). Nestboxes were undisturbed throughout the study except to remove the cub for weighing; this occurred approximately once every three days until the cub was 31 days old. At this time it was determined from baseline growth data that supplemental feeding was required for the cub. Esbilac formula was provided (in a 3:1 ratio with water) twice daily, and cub weight was then monitored daily until the cub was three months old.

Data were recorded on checksheets in 20 second intervals. The following variables were identified and recorded:

Female In Nestbox - the female enters a nestbox which contains the cub and remains for over 20 seconds. The nestbox occupied by the cub was noted each hour and any change was recorded as it occurred.

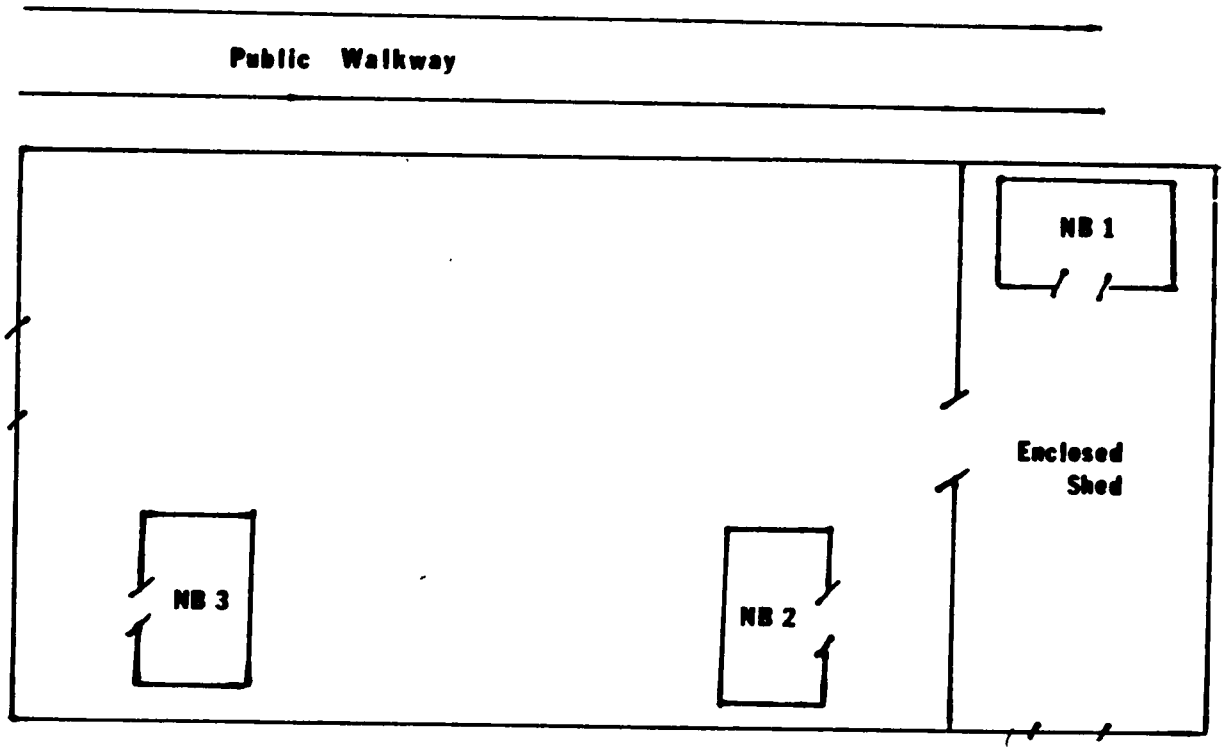


Figure 3.2 Diagrammatic representation of Enclosure #1 with emphasis on nestbox placement.

Female Out of Nestbox - the female leaves a nestbox containing the cub and remains out for over 20 seconds.

Nestcheck - the female enters a nestbox for less than 20 seconds or visually scans the inside of a nestbox while remaining outside.

Groom - the female licks the cub over various areas of its body, often interspersed with autogrooming. Pauses greater than one minute were recorded as separate bouts.

Female-Cub Rest - the female and cub lie together motionless or with periodic comfort movements (e.g., yawn, stretch, change position). Eyes are usually closed, although the female's tend to remain open for brief periods.

Cub Rest Alone - similar to above, except the cub is alone in the nestbox. Comfort movements of greater than 20 seconds duration were recorded as "Motion" (see below).

Suckle - measured bouts begin when the cub's mouth can be seen moving on the female's teat, and end with either the cub's mouth off the teat or termination of mouth movements. Additional bouts are measured when the cubs's mouth can not be seen clearly, but distinct

"smacking" noises can be heard, the cub is on the female's abdomen, and the female is definitely not grooming. These bouts end when noise ceases.

Motion - a general term for any cub movement which exceeds 20 seconds during the time the cub is alone in the nestbox. Specifics as to form of the motion (e.g., rocking, crawling using forelegs only, full crawl) were indicated on the observation sheet.

Vocalize - calls or cries uttered by either the female or the cub. Examples included the "whistle" previously described by Roberts (1981) and the "chitter" a contact call by the female (see Vocalizations , p. 76).

Carry - the female leaves the nestbox with the cub in her mouth.

Play - two forms were noted: Object play in which the cub manipulates straw or bamboo within the nestbox; and, Social play in which the cub and female interact utilizing a variety of behaviors such as pouncing, biting, wrestling, or rearing.

Environmental Factors - enclosure temperature and general climatic conditions (e.g., rain, thunder, bright sun) were noted each hour.

General Comments - notes concerning nonsystematically

determined factors which may have affected the animals' behavior were documented. Examples include: keeper entry, removal of cub for weighing or supplementary feeding, presence of viewing public, and construction.

Statistical Analysis of the data included Analysis of Variance, Mann-Whitney U, Regression Analyses, and t-Tests. Additional analyses (see `Nest Attendance and Preference') were performed using data collected by Dr. John Gittleman at the National Zoological Park (NZP) from 1982 to 1984. Three enclosures were observed in this study: #A, #98 and #1 (differentiated from the KZP enclosure #1 by being termed Enclosure #1 (NZP) when both are included in a Figure or Table). Nest attendance data for all enclosures were tested with both logged and unlogged data to record any change in the significance of the linear relationships.

Results and discussion

Data pertaining to nest attendance, nest preference, grooming and resting behavior, nursing bouts, and neonatal weight gain are reported and analyzed in a quantitative fashion. Other data mainly relating to behavioral positioning while resting, grooming, and nursing, are given subsequently in a separate section headed `Qualitative Results'.

Quantitative Results:

A. Nest Attendance and Nest Preference

Analyses of female nest attendance were performed using daily bout averages (totaled daily bout durations of Female In Nestbox divided by the number of bouts: see Fig.3.3), and log transformed bout averages. Regression analysis showed a significant negative correlation between duration of female in nest and cub age in both tests (bout avg.: $r = -0.38$, $n = 70$, $p < 0.001$; log transformed: $r = -0.46$, $n = 70$, $p < 0.001$). The data collected at NZP supported this finding: all three females similarly exhibited significant negative trends in time spent in the nest as their cubs aged (Fig. 3.4). Additional analyses were performed on the NZP enclosures utilizing log transformed bout averages in order to establish expected linearity in the relationship. The total number of bouts for all enclosures also were regressed on cub age. All tests were significant with the exception of the log transformed data of enclosure #98 (see summary: Table 3.1).

Enclosure temperature was found to have no effect on duration of nest attendance ($r = -0.08$, $n = 54$, $p > 0.05$). Female In bout averages for the KZP female were further tested in three 30 day intervals in order to more specifically determine the timing of decrease in

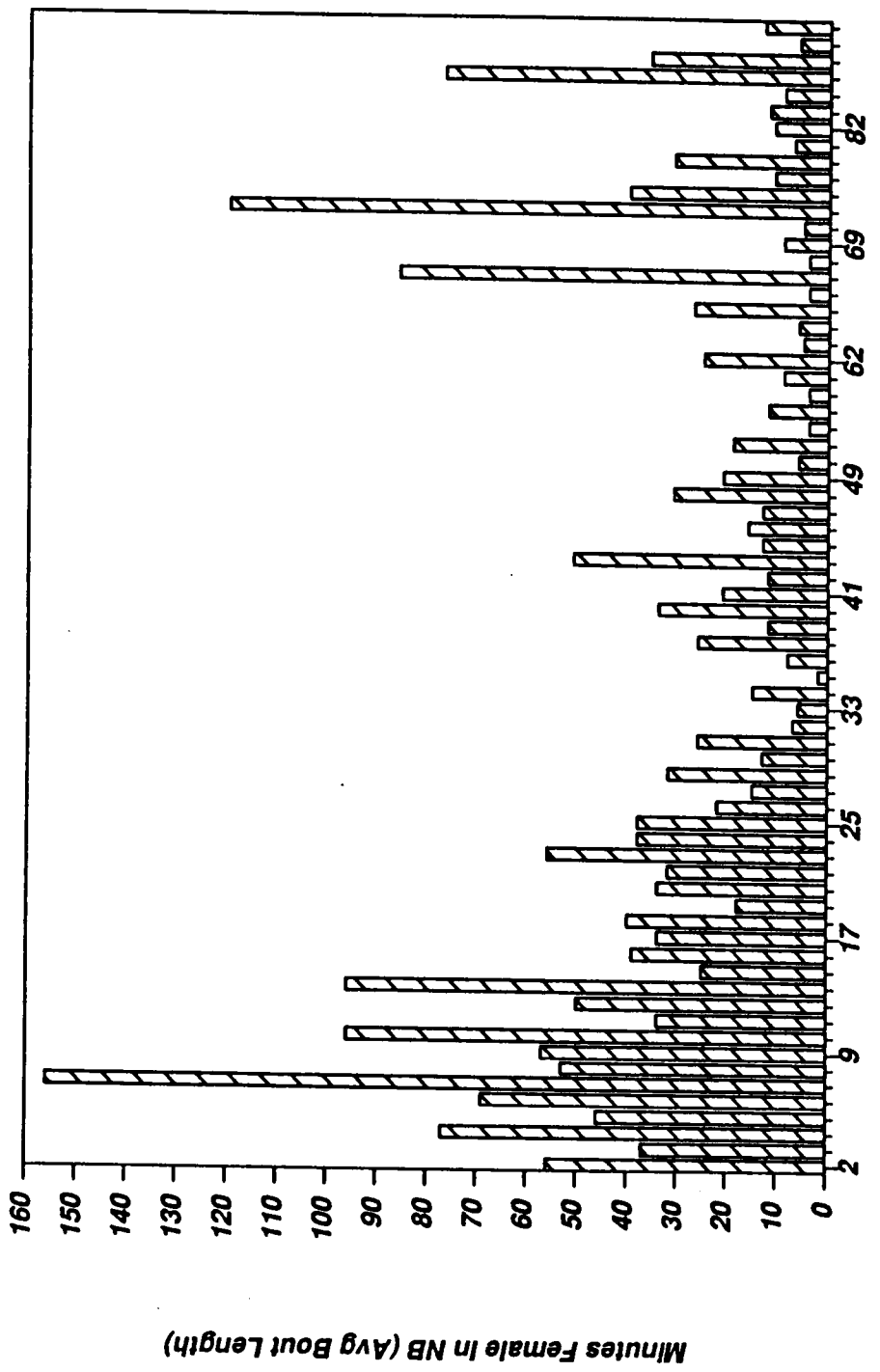


Figure 3.3 Daily bout length averages for time female spent in the nestbox plotted against cub age (days).

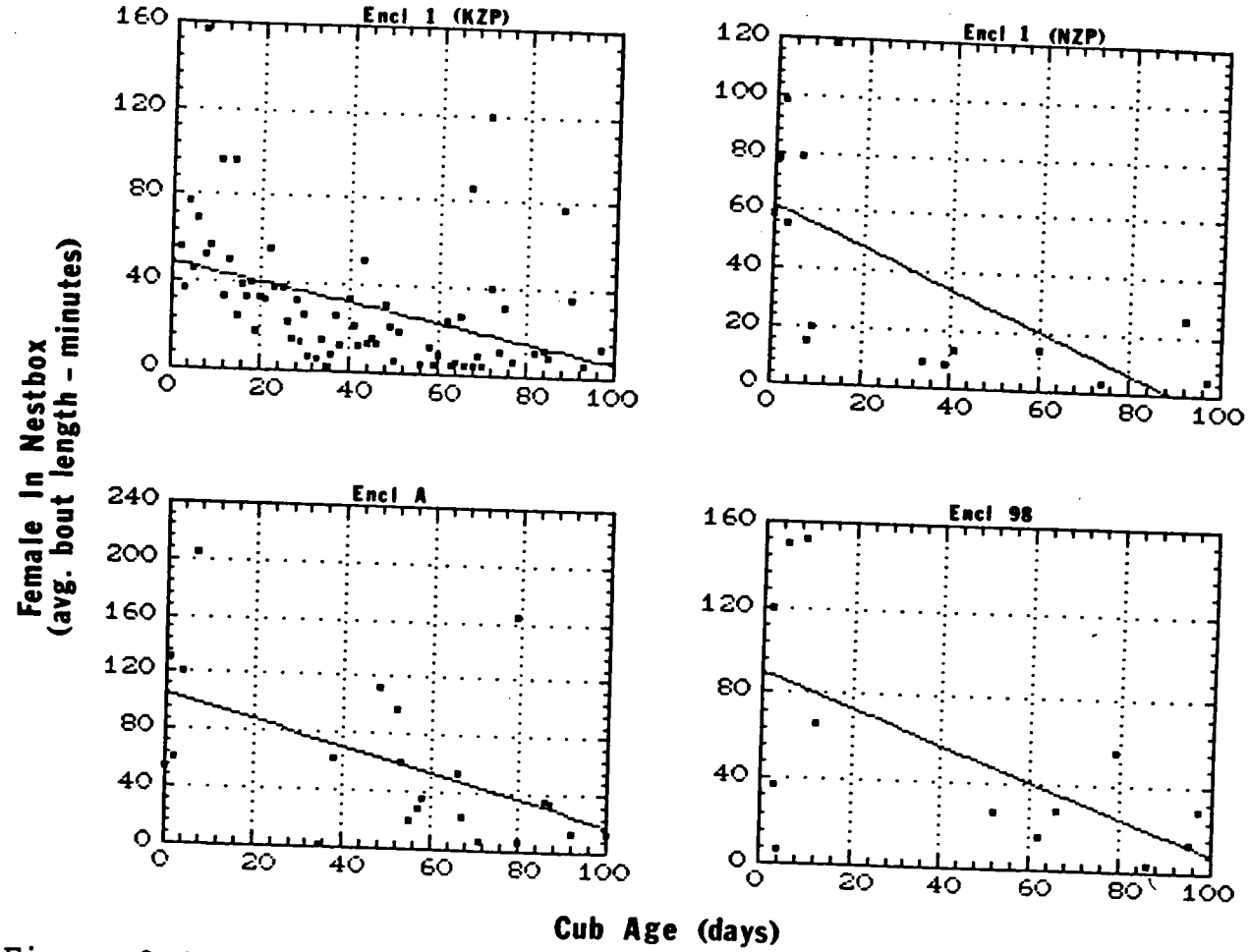


Figure 3.4 Regression of female in nestbox bout averages with cub age for KZP Enclosure #1, and NZP Enclosures #A, #98, #1.

Table 3.1 Female nest attendance summary statistics for logged and unlogged bout averages in all four enclosures.

	Enclosure	n	r	p value
Bout Averages	1(KZP)	70	-0.38	0.001
	1(NZP)	15	-0.62	0.01
	A	22	-0.50	0.01
	98	13	-0.6	0.05
Bout Averages (log transformed)	1(KZP)	70	-0.46	0.001
	1(NZP)	15	-0.71	0.01
	A	22	-0.43	0.05
	98	13	-0.52	0.10

nest attendance. Female In bout lengths averaged 47 minutes in the first 30 days ($n = 27$, $s = 30.5$), 15 minutes from day 31 to 60 ($n = 22$, $s = 11.7$), and averaged 26 minutes from day 61 to the end of the study ($n = 21$, $s = 31.4$).

There were significant differences in bout average length when the first 30 days were compared to both the 31-60 day interval and the 61-97 day interval ($t = 4.66$, $n = 49$, $p < 0.001$; $t = 2.42$, $n = 48$, $p < 0.02$ respectively). However, the last two intervals (days 31-60, 61-97) were not significantly different from one another ($t = -1.44$, $n = 43$, $p > 0.05$). Again, NZP data exhibited identical trends of high Female In bout averages within the first month which then declined significantly in the following two months (Enclosure #1 (NZP): $U = 2.0$, $n = 12$, $p < 0.05$; Enclosure A : $U = 5.0$, $n = 14$, $p < 0.05$; Enclosure 98 data was insufficient for this analysis).

Nestbox utilization by the female at KZP was tested for indications of preference. No preference for any single nestbox was observed. Out of a total 104 nestbox occupations, 34 (33%) were in nestbox #1, 32 (31%) in nestbox #2, and 38 (36%) in nestbox #3. There was, however, an obvious tendency for the female to exclusively utilize a nestbox for an extended period of time. Analysis of the data in two week intervals

showed that specific nestboxes were used during most intervals for over 50% of the time (Table 3.2).

Discussion:

In captivity, red pandas with cubs require at least two nestboxes (Conway 1981; Keller 1977; Roberts 1975; pers. obs.); this allows females to transfer cubs to another nest in the event of some nest disturbance. It was not possible to test for preference of particular nest sites in terms of nestbox size or configuration because nestboxes were identical. However, females utilize nests of sizes ranging from those just large enough for the female and her cubs to nests four times the females' body length (pers. obs.). Several characteristics have been cited as determinants of carnivore natal nest selection in the wild. These include nest dimension, entrance exposure, and entrance height from the ground (Schaller et al. 1985; Schneider et al. 1971). In captivity, lack of disturbance to the nest most likely plays the primary role in nestbox choice. Nest transfers did at times occur overnight when disturbances to the nest were unlikely, suggesting additional factors are involved. In the wild, raccoons (Procyon lotor) move nesting sites (Schneider et al. 1971) possibly in response to change in foraging locales. In captivity, red pandas may have a proclivity to move nest sites as a result of utilizing

Table 3.2. Comparisons of nestbox use during two week intervals.[a]

	%Use NB #1	%Use NB #2	%Use NB #3
Week 1-2	0	100	0
Week 3-4	0	11	89
Week 5-6	21	21	58
Week 7-8	66	25	9
Week 9-10	42	23	35
Week 11-12	63	10	27
Week 13-14	100	0	0

[a]%Use represents the number of times a particular nestbox (NB) was used divided by total number of nestboxes used during the interval.

different bamboo patches in the wild. Predator avoidance has additionally been cited as a reason for nest transfer in many carnivores (Ewer 1973). Although predation pressure is as yet unstudied with respect to red pandas in the wild, it must be included as a potential factor in nest choice and movement in captive animals.

In addition to nest selection and transfer, the amount of time a female spends attending the nest must be considered. Female red pandas with cubs have been observed to decrease the length of their nestbox visits by the sixth week of neonatal development (Roberts 1981). This study offers statistical support for that observation. Several factors are most likely involved in contributing to changes in the amount of time the female spends in the nest, though these factors were not isolated in the present study. Harper (1981) discusses several offspring characteristics which may play a role. In "hider" species or those which remain immobile and hide at an early age (e.g. some felids and ungulates, rabbits) the decline in mother-infant contact is dramatic. The first few days after birth are spent almost entirely with the litter, but thereafter contact is exclusively for nursing. Obviously, the red panda cannot be described as exhibiting this extreme in behavior, but the mechanisms

regulating a gradual decrease in contact after the first 30 days may be similar. Detailed experimental studies show that high levels of contact during the immediate postpartum period are necessary for maintenance of maternal behavior in rats and hamsters (review in Rosenblatt and Siegal 1983). Generally, most mammals switch from the "onset phase" of maternal behavior (prepartum to birth) to the "maintenance phase" (the period following birth) which involves a transition from maternal hormonal control to that of infant stimulus. After a brief but intense period of contact with their litters, maternal caregiving is maintained thereafter by periodic contact with the young. Thus, phase transition mechanisms may be involved in the decrease red panda nest attendance.

The gradual decrease in litter contact after the initial obvious drop may be related to changes in the offspring. Elicitation of maternal care may be due, as Lorenz (1971) suggests, to innate releasing mechanisms (IRM) characteristic of infants (e.g., relatively large head and eyes, clumsy movements, short and thick extremities). As the relatively large head and eyes, and distinct buff coloration of panda cubs are replaced by more characteristically adult traits, the female may then spend less time attending them. `Tear marks' or the dark bands running from the eye to the corner of

the mouth, were distinct by 16 days of age. The significant decline in female nest attendance did not occur until two weeks after the appearance of this characteristic adult trait. However, as an IRM may be dependant upon an entire suite of visual cues, it cannot be dismissed as a possibilty.

Leon et al.(1978) suggest that development of thermoregulatory ability may also contribute to decreasing nest attendance. Carnivore young tend to rest in contact with one another as a method of temperature regulation (Ewer 1973). The mother may be sensitive to changes in her offsprings' thermoregualtory ability, most likely via contact during nursing (Rosenblatt 1976; Smart 1983; Vince 1984). Thus, as thermoregulation becomes more efficient for offspring, the mother may spend less time in the nest.

The increased energetic demands placed on the female as the young develop also may have an effect on the time spent in caregiving. Gittleman (1988b) has shown that female red pandas, similar to other eutherian mammals (Gittleman and Thompson 1988), increase the duration of their feeding bouts during the lactation period. As development of the cubs continues and demands on the female increase, longer periods away from the nest may be spent in feeding.

Finally, the effect of litter size on maternal time budget should be mentioned. Captive studies on mongolian gerbils have shown an increase in time spent in the nest for single pup litters when compared with litters of three and five pups. However, maternal caregiving (in terms of grooming) was decreased and inactive time (resting with the litter) more frequent in single pup litters (Elwood and Broom 1978). Similar findings have been shown in mice (Priestnal 1972). The above studies offer the conclusion that smaller litters create less disturbance to the female, thus allowing her to spend more time in the nest. These studies do not, however, address the issue that in some cases larger litters necessarily require longer periods away from the nest spent in foraging due to the increased energetic demands upon the mother (see Gittleman and Thompson 1988 and above discussion). Therefore changes in nest attendance may be a reflection of maternal shifts in activity budget rather than an avoidance response to a larger litter. Another alternative is based again on thermoregulation. Huddling in larger litters is an effective means of maintaining offspring temperatures (Alberts 1978). In litters of one or two, however, the benefits gained by huddling may be relatively small without the female present. This would tend to increase the demand for maternal nest

attendance in smaller litters (Smart 1983). It would be interesting to determine if litter size has an effect on nest attendance in the red panda; however, since litter size does not vary considerably in this species, the difference in attendance may be difficult to discern.

B. Activities Within the Nestbox

Several behaviors occuring in the nest were also analyzed as daily bout averages. These included Grooming, Female-Cub Rest, and Cub Rest Alone, all observed exclusively in the KZP study.

Grooming bout lengths remained consistant throughout the study, on average four minutes per bout,(range 1-30 minutes; Fig 3.5). No correlation was found between the length of grooming and cub age ($r = 0.12$, $n = 70$, $p > 0.05$), or with the length of female nestbox visits ($r = 0.01$, $n = 70$, $p > 0.05$).

Since the total time the female spent in the nest had a significant effect on Female-Cub Rest bouts ($r = 0.68$, $n = 70$, $p < 0.001$), this was taken into account in the analysis of Female Cub Rest bouts by using the residuals of these variables and referring to this as Relative Female Cub Rest. The test of Relative Female-Cub Rest with Cub Age showed a slight positive correlation between the two ($r = 0.35$, $n = 70$, $p <$

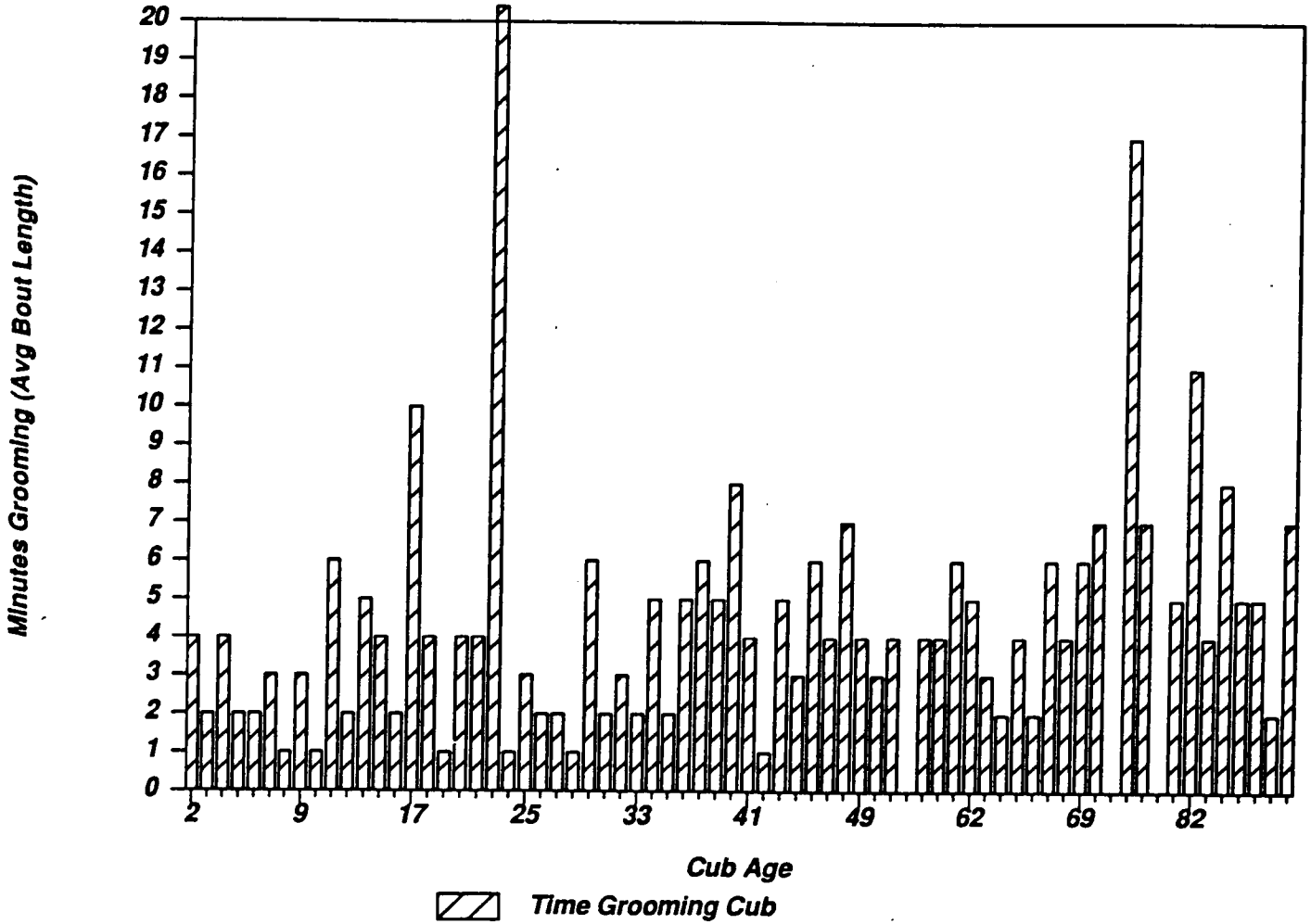


Figure 3.5 Daily bout length averages for time female spent grooming the cub plotted against cub age (days).

0.01). No significant effect was found between Cub Rest Alone and Cub Age ($r = 0.11$, $n = 70$, $p > 0.05$).

Discussion:

Consistant levels of grooming behavior have been cited as necessary for maintenance of mother-young recognition. The levels of grooming are usually low relative to other behaviors (e.g., resting) occuring in the nest (Elwood 1975; Konig 1985). Grooming also may ensure that the offspring are defecating as the female stimulates this process through licking the anourogenital region.

The fact that the red panda female did not decrease the amount of time spent resting with the cub but slightly increased this activity with cub age may again reflect the consequences of a small litter size (e.g., less disturbance to the female: Elwood and Broom 1978). An interesting possibility was outlined in a different context by Ewer (1968) in her discussion of ungulate "lying out" periods. Increased contact with the female may facilitate cub following behavior later in development. As the cub nears the time of nest emergence, the female may be encouraging close contact by the cub through longer resting periods together. Following behavior or close contact may then be more efficient once the cubs emerge from the nest.

C. Nursing

A total of 47 nursing bouts were observed. The average bout was three minutes in duration, with a range of one to 13 minutes (Fig. 3.6). No significant correlation was found between the amount of time the female spent in the nestbox and nursing bout length ($r = -0.19$, $n = 47$, $p > 0.05$).

Discussion:

Comparative studies have shown a direct relationship between growth rate and diet in carnivores (Gittleman and Oftedal 1987). The low nutrient quality of bamboo (Dierenfeld et al. 1982) may affect the quality and/or quantity of the red pandas' milk (Oftedal 1984) and thus contribute to reduced rate of growth. Milk composition has additionally been shown to influence the pattern of nursing. For example, aquatic mammals provide their young with concentrated, high energy milk which allows for short periods of lactation (Kovacs and Levigne 1986; Robbins 1983). If the red panda produces a poor quality milk, as has been hypothesized (Gittleman and Oftedal 1987), then the time devoted to nursing would necessarily be longer. This requirement could be met by exhibiting short but frequent suckling periods, or long less frequent bouts. Although the greatest number of bouts seen in one day was four (at 48 days of age), the short length of all



Figure 3.6 Duration of nursing bouts in relation to cub age (days).

observed suckling periods and the brief nest visits by the female suggest the former nursing pattern. Nevertheless, many nursing bouts were likely missed while the cub was offscreen and/or during the female's nocturnal visits to the nest. Also, supplemental feeding could have affected the frequency and/or length of nursing bouts; therefore these data should be considered preliminary.

D. Cub Weights

Weight gain by the cub began at an extremely low rate. For the first month average weight gain was approximately three grams/day. After milk supplements began (at 31 days of age), weight gain increased in the following month to 15 grams/day; it further increased to a gain of 25 g/day from age 60 to 90 days (Fig. 3.7).

Discussion:

The growth rate of red pandas is slower than any other carnivore species. Most likely this is due to the diet of bamboo, as discussed previously (Gittleman and Oftedal 1987). Average growth rate of neonates during the nestbound stage is 7-20 grams/day (Conway 1981; Roberts 1975; Roberts and Gittleman 1984; Roberts and Kessler 1979; Watson and Barfield 1982). Previous litters sired by the female in Enclosure #1 maintained

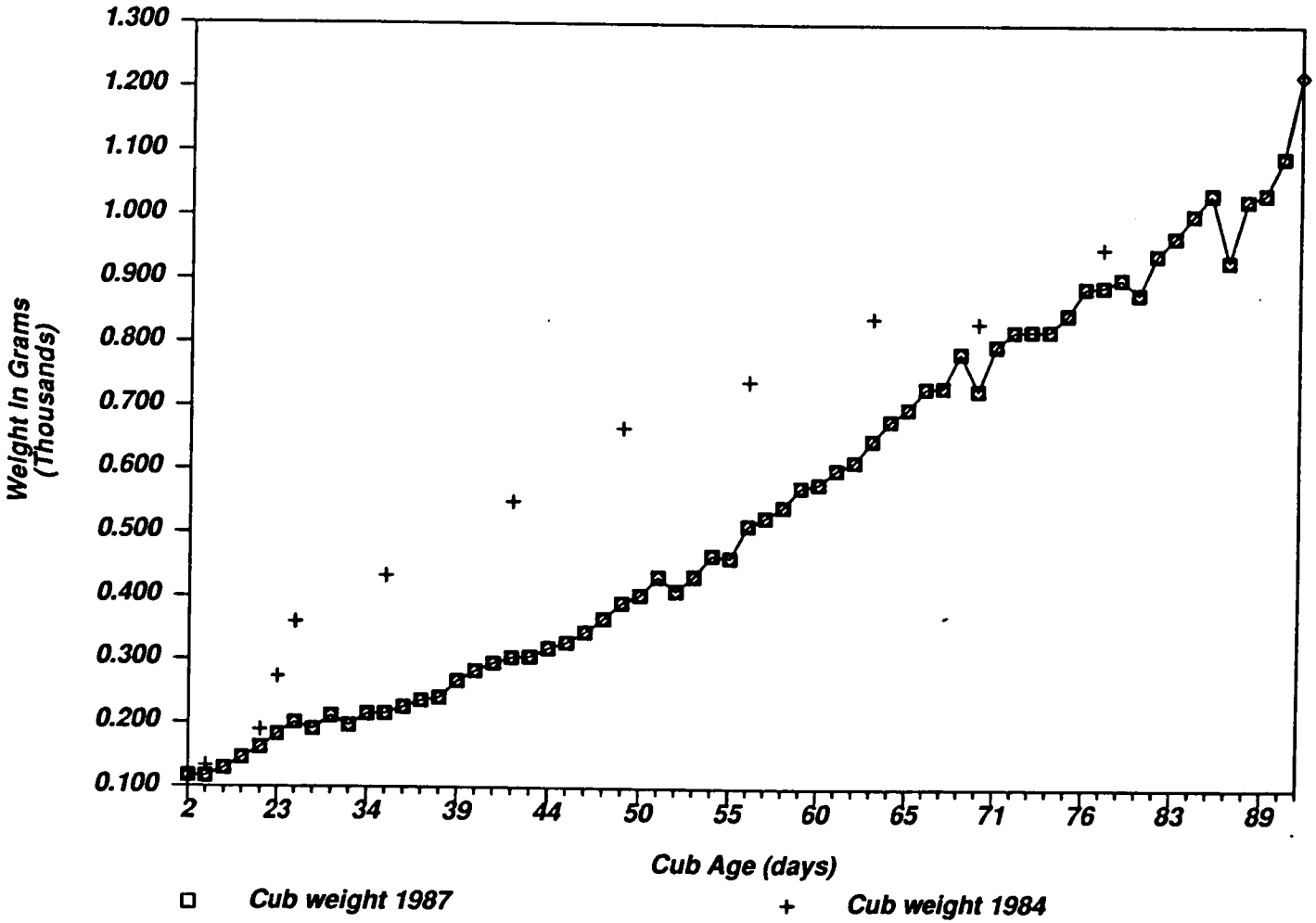


Figure 3.7 Cub weight gain as measured through the study. (*) indicates day supplemental feeding began. All weight measurements were collected prior to feeding.

the average rate of growth (as determined from other growth trajectories) from bh (see Fig 3.7, dotted line). However, milk supplements were required for the 1987 cub in order to achieve this rate of growth. The cub's growth rate, indeed, increased beyond the 7-20 grams/day "norm", attaining a 25 gram/day weight gain rate in the last 20 days measured. As mentioned in Chapter III (see`Methods'), a second litter born at KZP suffered a fatality. The second littermate was recovered and successfully handraised although it too had severely dropped in weight. These examples raise questions concerning the ability of females to transfer energy (via milk) to their young. It has been demonstrated in several carnivore species that hand raised individuals attain much faster rates of growth than do their mother-reared counterparts (for review see Gittleman and Oftedal 1987). The red panda seems to be no exception; higher growth rates can be attained with milk supplements. Thus, support is gained for the idea that slow growth rate in red pandas is due to the limiting factor of poor quality milk.

Qualitative Results:

A. Female Positions for Resting, Grooming, and Nursing

Several resting postures were used by the female while she occupied the nest. A side curled position

was assumed most often by the female during the early part of cub development. At this stage the cub was small enough to be encircled by her body. This position remained a common one, however, as the cub grew it became more visible lying at the female's abdomen or neck region. A second posture, assumed less frequently, was one in which the female rested on her back. The cub generally laid on her mother's abdomen, but could also be found resting near the female's side or draped over her legs.

Since many grooming episodes took place in between bouts of Female-Cub Rest, many of the postures used by the female for grooming were variations of rest postures. If the female, for example, was resting on her side with the cub by her abdomen, grooming would most often occur in this same position. Similarly, if the female was resting on her back, she would merely raise her head and shoulders to groom the cub lying on her abdomen. In both grooming postures the female would manipulate the cub with her paws, turning it frequently to groom different areas of the body. Grooming bouts occuring at times other than after a Female-Cub Rest bout (e.g. immediately following the female's entry into the nest), were generally characterized by two other postures. In the first, the female would remain standing, straddle the cub with her

front paws, and bend her head to groom. A second posture consisted of the female sitting near the cub to groom. Both of these postures allowed for less manipulation of the cub by the female. Mutual mouth licking or "mouth suckling" occured during grooming bouts. This has been hypothesized in other mammals to be involved in the introduction of solid foods to the young by either "giving them the taste" of their diet-to-be (e.g., bamboo) or by transference of bacteria needed for digestion (Ewer 1973).

Nursing postures assumed by the female were similar to those of rest: she would either curl around the cub while on one side, or lie on her back with the cub on her abdomen. Of the bouts observed (n = 47), all were initiated by the female. She would do so by pulling the cub toward her teat, and repeating the process until suckling or teat seeking began by the cub. Teat seeking in the cub took the typical carnivore form (Adamson 1969; Ewer 1961, 1963; Rheingold 1963) of side to side head motions performed until the teat was located. Once the cub attached to the nipple movement was limited to jaw motions. No evidence of a milk tread or other milk flow facilitating movements were observed. Termination of nursing bouts occured when the cub fell off the teat asleep, fell asleep and remained on the teat, or

voluntarily detached and resumed some other activity (e.g., play, rest). The female was never observed to actively reject the cub from a nursing episode.

No teat preference was exhibited by the cub. All four teats were used during the bouts observed. Additionally, during several of the nursing bouts the cub moved from one teat to another.

Discussion:

Conclusions drawn with respect to initiation and termination of nursing bouts in red pandas may be limited, as supplemental feeding probably affected the cub's motivation to nurse. However, factors such as teat preference and milk facilitation behavior do not seem as likely to have been affected. The lack of teat preference in the cub may merely be due to the small litter size. As there was no competition for a teat, a factor shown to play a significant role in maintenance of nursing order in domestic pigs (Hartsock et al. 1977), selection by the cub for a particular teat does not seem likely. Studies with larger litters will be necessary in order to determine if teat preference is evident.

B. Vocalizations

Two vocalizations were recorded as performed by the cub, however the intensity with which they were

emitted may be the only difference between them. One has previously been described by Roberts (1981) as a "whistle" - a high amplitude distress call heard by cubs during situations such as handling by keepers, or after falling from the nest. The cub observed in this study did not emit the whistle frequently, however, when it did occur it was normally in response to female carrying behavior or keeper handling. The second vocalization occured very frequently. It consisted of a series of short, low amplitude calls performed most often when the cub was left alone by the female. If the female was within hearing distance it normally served to reestablish contact between the two, thus serving a similar function to the whistle (Roberts 1981). Cub vocalizations occured most often in the first five days of age. They were calls primarily in response to female entry or exit from the nest. The vocalizations occured throughout the study, although after the cub reached six weeks of age they were heard infrequently and only in response to being carried by the female.

The female also performed a contact call not previously described. It was termed a "chitter" due to its similarity with that emmitted by female raccoons (Seiber 1986) and its descriptiveness in terms of the sound of the call. The chitter occured primarily upon

the female's entrance to the nest. It was most often performed before the cub vocalized, however, it also occured in response to the cub's call.

Discussion:

Mother-infant vocalizations in red pandas are strikingly similar to Seiber's (1986) description of raccoon mother/cub contact calls. The term "chitter" is also used for the raccoon maternal call which functions in announcing entrance to the nest, responding to cub cries, and later as a leading call during excursions from the nest. Again, functional similarity is found with the red panda "chitter". For the cub's first month of age the chitter was primarily a response call to distress vocalizations from the cub. Subsequent to this, however, the female initiated contact by signalling her entry into the nest; chittering without a prior cub call. During the cub's first excursions from the nestbox, the female was often heard chittering to the cub before picking it up and returning it to the nest. The contact call emitted by the cub was most similar to the raccoon cubs' "whistle" which serves as a response to the female's chitter and as a low key distress call bringing the female to the nest. A final raccoon vocalization termed a "squeal" is equivalent to Roberts (1981) "whistle" - it is a

neonatal severe distress call often referred to as a "wheet".

C. Motor Development

Development of motor skills by the cub was a gradual process. However several distinct changes were noted:

Behavior	First occurance
Rocking on all four legs -	3 days
Pulling body by forelimbs -	5 days
Hind limb use -	41 days
Coordinated crawl -	60 days
Self grooming -	66 days
Rear up on hindlimbs -	72 days
Running -	85 days
`Hesitant' tree climbing -	89 days

Present throughout the entire study were behaviors broadly grouped as "comfort movements". These included yawning, stretching, body twitching, curling, and one noted at day 25, chewing (in sleep).

D. Play

Observations of play within the nestbox were infrequent, however those behaviors that were observed were catagorized as follows:

Object Play - the first instance in which object play was observed was at 62 days. Straw within the

nest was manipulated by the cub with all four legs while she rolled on her back. At times the cub drew some straw into her mouth with biting motions, yet it was not clear if any straw was consumed. In the same episode, the cub began to play with her toes. This involved chewing on and grasping of her own feet. This type of solitary play was observed until the end of the study.

Social Play - since the cub was a singleton, social play within the nest was between the cub and the female. The male in the enclosure never entered a nestbox containing the cub during the course of the study. Social play between the cub and female was not observed until cub age of 66 days. Only three bouts of social play were observed in the nest. Play between the cub and female could best be described as a one sided rough and tumble. The cub would direct a series of bites and pounces toward the female as she parried while lying on her back. During the entire sequence no vocalizations were heard from either the cub or the female. It was also during these play bouts that the cub exhibited "rearing" behavior or upright posture on the hind legs (Gittleman 1985b). This usually preceded a pounce at the female. Occasionally the two would wrestle, however, the female had limited space in the nestbox for movement which may have hindered this type

of play.

Discussion:

Most likely one of the primary reasons such low frequencies of play behavior were observed in the study was the slow development of motor skills in the cub. Play has been hypothesized to be energetically costly (Burghardt 1984, 1988; Martin 1982, 1984). Therefore, in order for play to be a frequent behavior within a species it must be able to "afford" the cost. Recent comparisons of carnivores have shown dietary influences on the rate of metabolism. Folivorous species such as the red panda exhibit the lowest basal metabolic rates among carnivores (McNab 1988). Thus a metabolically constrained animal such as the red panda would be expected to show low levels of play behavior. A second factor which may have effected the frequency of play was the small litter size. Mendl (1988) has shown a quantitative and qualitative difference in the play experiences of domestic kittens in litters of two versus those in single kitten litters. Although there was no difference between litters in the amount of object play, the frequency and form of social play was significantly different. Single kitten litters received higher levels of maternal play than did litters of two; yet overall the single kittens received much lower frequencies of social play due to high

levels of maternal avoidance. Again, comparisons with varying litter size in red pandas would be interesting to observe to discern the potential differences in frequency of social play.

E. Carries

The female first carried the cub at 19 days of age. She carried it in this instance 14 times, the highest number of carries recorded in the study. Carries were observed on 15 other occasions, the last occured when the cub was 11 weeks old.

Discussion:

Carrying behavior most often occurred in response to nest disturbance. Eight out of the 15 carrying bouts took place immediately following the return of the cub to the nest after weighing or supplemental feeding by the keepers. Construction near the enclosure accounted for two observed bouts. The final three carrying episodes observed were attempts by the female to keep the cub in the nest after it had crawled out into the enclosure (see below).

F. Emergence

Roberts and Gittleman (1984) report that red panda cubs first emerge from the nest at around 90 days of age and usually at night. Since nocturnal observations were not carried out, the first recorded excursion was

during the day when the cub was 74 days of age. The female had previously taken the cub out into the enclosure at 62 days, during which time the cub explored her surroundings until the female returned it to the nestbox. In the week following this maternal initiated excursion, the cub repeatedly attempted to crawl out of the nest but was unable to do so because the cub was placed by the female in an elevated nestbox (approximately 2 meters off the ground). On day 74 the female had moved the cub to nestbox #3 (one located directly on the ground) and the cub was able to emerge from the nest on her own. By 85 days of age the cub was able to climb out of the elevated nestbox as well.

Discussion:

Montgomery et al. (1970) report similar behavior in wild raccoons. The female they observed moved her young from a tree to a ground nest after their first attempts at leaving on their own. They hypothesized that the female was responding to the increasing activity levels of her cubs, and so moved them to prevent injury. Once the red panda cub was returned to the nest the female would immediately groom the cub for long periods of time (10-15 minutes). Continued periods of tactile stimulation have been shown in rats to have the effect of reducing behavioral activity (Hofer 1981). This was evident in the red panda as

well, for the cub would usually fall asleep during these bouts of grooming. Thus, the female may prevent her cubs from leaving the nest by pacifying them until motor coordination skills necessary for life outside the nest have been developed.

Summary

1. Females significantly decrease the amount of time spent in the nest after their cubs' first month of life. Temperature was shown to have no effect on nest attendance, however, the decrease may relate to changes in the thermoregulatory ability of the litter, size of the litter, or a change in the energetic demands placed on the mother.

2. Maternal grooming bouts remained at consistant, low levels through the cub's nestbound stage; this facilitated cub defecation and may have served to maintain mother-young recognition. Female/cub resting bouts increased with cub age, perhaps to encourage future close contact between the mother and the cub during emergence.

3. The amount of time the female spent in the nest had no significant effect on the duration of nursing. Nursing periods were of short duration in comparison to nursing bouts observed in other carnivores. Brief nursing bouts accompanied with the

assumption of short interbout intervals is consistant with the hypothesis that red pandas produce poor quality milk.

4. The rate of cub weight gain (from 30-97 days of age) substantially increased through the use of milk supplements, again emphasizing the potential limiting factor of poor quality milk on cub growth.

5. No teat preference or milk facilitation behavior was exhibited by the cub. This may be due to the singleton's lack of competition from other littermates.

6. Calls between the female and cub seemed to function in establishing contact between the pair and were similar to those reported for raccoons (Procyon lotor).

7. Play behavior occured at low frequencies, perhaps due to slow motor development in the cub, energetic constraints, or small litter size.

8. Cub emergence was observed at 74 days of age. Lengthy maternal grooming bouts most likely prevented the cub from leaving the nest prior to this.

LIST OF REFERENCES
CHAPTER III

Adamson, J. 1969. The Spotted Sphinx. London: Collins and Harvill Press.

Alberts, J.R. 1978. Huddling by rat pups: group behavioral mechanisms of temperature regulation and energy conservation. J. Comp. Physiol. Psych., 92, 231-245.

Barrett, P. and Bateson, P. 1978. The development of play in cats. Behaviour, 66, 106-120.

Bekoff, M. 1988. Behavioral development in terrestrial carnivores. In: Carnivore Behavior, Ecology and Evolution (Ed. J.L. Gittleman), Ithaca, New York: Cornell Univ. Press (in press).

Biben, M. 1983. Comparative ontogeny of social behaviour in three South American canids, the maned wolf, crab-eating fox, and bush dog: implications for sociality. Anim. Behav., 31, 814-826.

Burghardt. G.M. 1984. On the origins of play. In: Play in Animals and Humans (Ed. P.K. Smith), pp. 5-41. Oxford, England and New York: Basil Blackwell.

Burghardt, G.M. 1988. Precocial behavior, play and the ectotherm - endotherm transition: profound reorganization or superficial adaptation? In: Handbook of Behavioral Neurobiology, Vol. 9 (Ed. E.M. Bass), pp.107-148. New York and London: Plenum Press.

Burghardt, G.M. and Burghardt, L.S. 1972. Notes on the behavioral development of two female black bear cubs: the first eight months. In: Bears - their Biology and Management (Ed. S. Herrero), pp.253-273. I.U.C.N. Report #23, Morges, Switzerland.

Caro, T.M. 1987. Indirect cost of play: cheetah cubs reduce maternal hunting success. Anim. Behav., 35, 295-297.

Conway, K. 1981. Supplemental feeding of maternally reared red pandas Ailurus fulgens. Int.. Zoo Yb.., 21, 236-239.

Dierenfeld, E.S., Hintz, H.F., Robertson, J.B., VanSoest, P.J. and Oftedal, O.T. 1982. Utilization of bamboo by the giant panda. J. Nutr., 112,636-641.

Eaton, R.L. 1974. The Cheetah: the Biology, Ecology and Behavior of an Endangered Species. New york: Litton Educational Publishing.

Eisenberg, J.F. 1981. The Mammalian Radiations.Chicago: Univ. of Chicago Press.

Elwood, R.W. 1975. Paternal and maternal behavior in tne Mongolian gerbil. Anim. Behav., 23,766-772.

Elwood, R.W. and Broom, D.M. 1978. The influence of litter-size and parental behaviour on the development of Mongolian gerbil pups. Anim. Behav., 26,438-454.

Ewer, R.F. 1961. Further observations on suckling behaviour in kittens, together with some general considerations of the interrelations of innate and aquired responses. Behaviour, 18, 247-260.

Ewer, R.F. 1963. A note on the suckling behaviour of the viverrid, Suricatta suricata (Schreber). Anim. Behav., 11, 599-601.

Ewer, R.F. 1968. Ethology of Mammals. New York and London: Plenum Press.

Ewer, R.F. 1973. The Carnivores. Ithaca, New York:Cornell University Press.

Gittleman, J.L. 1985a. Functions of communal care in mammals. In: Evolution: Essays in Honour of John Maynard Smith (Eds. P.J. Greenwood, P.H. Harvey and M. Slatkin), pp. 187-205. Cambridge: Cambridge Univ. Press.

Gittleman, J.L. 1985b. Final report submitted during tenure as a Smithsonian Postdoctoral Fellow.

Gittleman, J.L. 1988a. Carnivore Behavior, Ecology and Evolution. Ithaca, New York: Cornell Univ. Press (in press).

Gittleman, J.L. 1988b. Behavioral energetics of lactation in a herbivorous carnivore, the red panda (Ailurus fulgens). Ethology (in press).

Gittleman, J.L. and Oftedal O.T. 1987. Comparative growth and lactation energetics in carnivores. Symp. Zool. Soc. Lond., 57,41-77.

Gittleman, J.L. and Thompson, S.D. 1988. Energy allocation in mammalian reproduction. Amer. Zool. (in press).

Gray, B.J. 1970. Care and development of a hand-reared red panda. Int. Zoo Yb., 10,139-142.

Harper, L.V. 1981. Offspring effects upon parents. In: Parental Care in Mammals (Eds D.J. Gubernick and P.H. Klopfer), pp.117-177. New York and London: Plenum Press.

Hartsock, T.G., Graves, H.B. and Baumgardt, B.R. 1977. Agonistic behavior and the nursing order in suckling piglets: relationships with survival, growth and body composition. J. Anim. Scien., 44, 320-330.

Heidt, G.A. 1970. The least weasel Mustela nivalis Linnaeus, developmental biology in comparison with other North American Mustela. Mich. St. Univ. Biol. Ser., 4,227-282.

Hofer, M.A. 1981. Parental contributions to the development of their offspring. In: Parental Care in Mammals (Eds. D.J. Gubernick and P.H. Klopfer), pp. 77-115. New York and London: Plenum Press.

Keller, R. 1977. Beitrag zur ethologie des kleinen pandas (Ailurus fulgens, Cuvier,1825). Unpublished Ph.D. dissert., Univ. Zurich, Switzerland, 122pp.

Kleiman, D.G. 1983. Ethology and reproduction of captive giant pandas (Ailuropoda melanoleuca). Z. Tierpsychol. 62, 1-46.

Kleiman, D.G. and Eisenberg, J.F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav., 21, 637-659.

Kleiman, D.G. and Malcolm, J.R. 1981. The evolution of male parental investment in mammals. In: Parental Care in Mammals (Eds. D.J. Gubernick and P.H. Klopfer), pp.347-387. New York and London: Plenum Press.

Konig, B. 1985. Maternal activity budget during lactation in two species of Caviidae (Cavia porcellus and Galea musteloides). Z. Tierpsychol. 68,215-230.

Kovacs, K.M. and Levigne, D.M. 1986. Maternal investment and neonatal growth in phocid seals. J. Anim. Ecol., 55, 1035-1051.

Leon, M., Croskerry, P.G. and Smith, G.K. 1978. Thermal control of mother-young contacts in rats. Physiol. Behav., 21, 793-811.

Lorenze, K. 1971. Part and parcel in animal and human societies (1950): a methodological discussion. In: Studies in Animal and Human Behavior Vol.II (Ed. R. Martin), pp 115-195. Cambridge: Harvard Univ. Press.

McNab, B.K. 1988. Rate of metabolism, body size, and food habits in the order Carnivora. In: Carnivore Behavior, Ecology and Evolution (Ed. J.L. Gittleman), Ithaca, New York: Cornell University Press, (in press).

Martin, P. 1982. The energy cost of play: definition and estimation. Anim. Behav., 30, 294-295.

Martin, P. 1984. The time and energy costs of play behaviour in the cat. Z. Tierpsychol., 64, 298-312.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. Anim. Behav., 25, 1-9

Mendl, M. 1988. The effects of litter-size variation on the development of play behaviour in the domestic cat: litters of one and two. Anim. Behav., 36, 20-34.

Mertl-Millhollen, A.S., Goodman, P.A., and Klinghammer, E. 1986. Wolf scent-marking with raised-leg urination. Zoo Biol., 5, 7-20.

Montgomery, G.G. 1969. Weaning of captive raccoons. J. Wildl. Mgmnt., 33, 154-159.

Montgomery, G.G., Lang, J.W. and Sunquist, M.E. 1970. A raccoon moves her young. J. Mammal., 51, 202-203.

Oftedal, O.T. 1984. Milk consumption, milk yield and energy output at peak lactation: a comparative review. Symp. Zool. Soc. Lond., 51, 33-85.

Peking Zoo 1974. On the breeding of the giant panda and the development of its cubs. Acta Zool. Sinica, 20, 386-394.

Pond, C.M. 1977. The significance of lactation in the evolution of mammals. Evolution, 31,177-199.

Priestnal, R. 1972. Effects of litter-size on the behaviour of lactating female mice (Mus musculus). Anim. Behav., 20, 386-394.

Rheingold, H.L. (Ed.) 1963. Maternal Behavior in Mammals. New York and London: John Wiley and Sons.

Robbins, C.T. 1983. Wildlife Feeding and Nutrition. New York and London: Academic Press.

Roberts, M.S. 1975. Growth and development of mother-reared red pandas. Int. Zoo Yb., 15,57-63.

Roberts, M.S. 1981. The reproductive biology of the red panda, Ailurus fulgens, in captivity. Unpubl. M.S. thesis, Univ. Maryland, 202 pp.

Roberts, M.S. and Gittleman, J.L. 1984. Ailurus fulgens Mammalian Species Account No. 222, pp. 1-8.

Roberts, M.S. and Kessler, D.S. 1979. Reproduction in red pandas, Ailurus fulgens (Carnivora: Ailuropodidae). J. Zool., 188, 235-249.

Rosenblatt, J.S. 1976. Stages in the early behavioral development of altricial young of selected species of non-primate mammals. In: Growing Points in Ethology (Eds. P.P.G. Bateson and R.A. Hinde), pp. 345-383. Cambridge: Cambridge University Press.

Rosenblatt, J.S. and Seigal, H.I. 1983. Physiological and behavioural changes during pregnancy and parturition underlying the onset of maternal behaviour in rodents. In: Parental Behaviour of Rodents (Ed. R.W. Elwood), pp.23-66. New York: John Wiley and Sons.

Ryon, J. 1986. Den digging and pup care in captive coyotes (Canis latrans). Can. J. Zool. 64, 1582-1585.

Schaller, G.B., Jin Chu, H., Wenshi, P., and Jing, Z. 1985. The giant pandas of Wolong. Chicago: Univ. of Chicago Press.

Schneider, D.G., Mech, D.L. and Tester, J.R. 1971. Movements of female raccoons and their young as determined by radio-tracking. Anim. Behav. Monogr., 4, 1-43.

Seiber, O.J. 1986. Acoustic recognition between mother and cubs in raccoons (Procyon lotor). Behaviour, 96, 130-163.

Smart, J.L. 1983. Undernutrition, maternal behavior, and pup development. In: Parental Behavior of Rodents (Ed. R.W. Elwood), pp. 205-234. New York: John Wiley and Sons.

Trivers, R.L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man, 1871-1971 (Ed. B. Campbell), pp.136-179. Chicago: Aldine.

Vince, M.A. 1984. Teat-seaking or pre-suckling behaviour in newly-born lambs: possible effects of maternal skin temperature. Anim. Behav., 32, 249-254.

Watson, J.K. and Barfield, V.L. 1982. Supplemental feeding of infant red pandas at the Knoxville Zoological Park. In: The Red or Lesser Panda Studbook (Ed A.R. Glaston), pp. 29-35. The Royal Rotterdam Zoological and Botanical Gardens Rotterdam, The Netherlands.

Wemmer, C.M. 1977. Comparative ethology of the large spotted genet (Genetta tigrina) and some related viverrids. Smithsonian Contrib. Zool., 239, 1-93.

CHAPTER IV

CONCLUSION

To facilitate concluding comments of red panda reproductive behavior it is necessary to reiterate the results and conclusions from the two preceding chapters. In the scent-marking study, individuals of both sexes showed significant preferences for scent-marking particular locations, especially prominent points, in each enclosure. Males scent-marked more and in a different fashion than females, although female marking was greater in this study than in previous reports. Females were found to increase marking frequency during the breeding period. However, males were not observed to increase scent-marking, perhaps because outside of breeding male marking behavior was considerably frequent. Certain behavioral features were associated with scent-marking behavior. For example, the number of waddles (defined as each anogenital motion) was positively correlated with duration of scent-marking; and individuals of each sex preferentially sniffed marking areas of the other sex.

In terms of maternal care and neonatal development, females significantly decreased the amount of time spent in the nest after their cubs' first month

of life. Temperature was shown to have no effect on nest attendance. Maternal grooming bouts remained at consistant, low levels through the cub's nestbound stage and this may have facilitated cub defecation. Female/cub resting bouts were found to increase with cub age. In terms of nursing behavior, the amount of time the female spent in the nest had no significant effect on the duration of nursing; nursing periods were frequent and of short duration; and, no teat preference or milk facilitation behavior was exhibited by the cub. Calls between the female and cub seemed to function in establishing contact between the pair and were similar to those reported for raccoons (Procyon lotor). Play behavior was observed in two forms: solitary object play and mother-cub social play; however, both forms occured only in low frequencies. Similar to other carnivores, substantial increases in the rate of cub weight gain were achieved with milk supplements. Cub emergence was observed at 74 days of age. Lengthy maternal grooming bouts prevented the cub from leaving the nest prior to this.

In this concluding chapter I will discuss these results in relation to considerations of: 1) the restrictions imposed on these data due to study in captivity; 2) the effects of social structure and feeding strategy on scent-marking in red pandas; 3) the

effects of social structure and feeding strategy on maternal care and neonatal development; and, 4) future research goals.

A. Problems in captive behavorial research:

In discussing overall conclusions of this study it is necessary to mention that trends observed in both scent-marking and maternal care may have been effected by the captive setting. Factors present in captivity which differ from wild populations include: 1) artificially imposed social structures, 2) environments limited in natural complexity, 3) scheduled and regular feeding regimens, 4) presence of viewing public, and 5) lack of predation pressure (Burghardt 1975; Eisenberg and Kleiman 1977; Gittleman and Conover in press; Markowitz 1975). These problems, common to all studies performed in captivity, were accompanied by issues faced more specifically by the current study. The problems to acknowledge here include:

1) Presence of an observer during the scent-marking watches - although the pandas calmed after the first few minutes of observation (see Jordan and Burghardt 1986), it is possible that behavior could have been subtly affected by data collection near the enclosure.

2) Difference in the topography and size of the

enclosures - enclosure #4, observed in the scent-marking study, was unique in its partial division by a fence through the center. This may have effected the marking site preferences of male and female #4. The potential effect was reflected by the male's prefered site (#4) being located on the opposite side of the division from the female's (#13). The size of the enclosures (10x4x6 meters) may have influenced behavior patterns primarily observed during the scent-marking study. Stereotypic pacing behavior, in which certain pathways are paced continuously, was occasionally observed. As marking occured during these episodes, a bias toward sites located on the pathways may potentially result and thus mistakenly be termed a "prefered site".

3) Presence of keepers for feeding and cleaning - the effect of keeper presence was evident in both studies. During keeper entry for feeding, activity levels of the pandas increased which may have influenced scent-marking rates (but see Gittleman 1988a). Cleaning marking sites has also been shown to effect the incidence of marking on those sites (Moran and Sorensen 1986). Marking site cleaning, however, did not occur on a regular schedule to enable testing of this effect on red panda scent-marking. The presence of keepers may also have effected nest attendance in that

the female left the nest to feed immediately after bamboo was placed in the enclosure. No visible effect on the female could be discerned by presence of the keepers for cleaning, however, subtle changes in behavior may have gone unnoticed.

4) Presence of the viewing public - public walkways run within two meters of the red panda enclosures. While large crowds (10-15 people) would periodically aggregate, this seemed to have little effect on the activity of red pandas at KZP which appear to have adapted to closer scrutiny than pandas at other zoos (Gittleman pers. comm.).

5) Provision of milk supplements - this probably effected the cub's motivation to nurse from the mother, thus decreasing the frequency and/or duration of observed nursing bouts.

6) Daily cub handling for above-mentioned milk provisioning and to obtain cub weights - frequently during these handling episodes, the cub would emit distress calls which seemed to agitate the female (see Roberts 1981). As the cub was placed back into the nest, the female would invariably enter and groom the cub or carry it to another nest (this occured less frequently). These "stress induced" female-cub contacts may have had some effect on the recorded time of female nest attendance.

7) Construction outside of the enclosures - during one week of the maternal care study, large machines (e.g. backhoes) were driven near the enclosure for construction. The effect on the female was apparent in that she carried the cub from nest to nest for durations of up to 30 minutes and at a frequency higher than any other throughout the rest of the study.

Although these factors may have affected the behavioral events and sequences recorded in the study, it can be argued that information gained about red panda reproductive behavior (e.g. scent-marking behavior during the breeding period, mother-cub interactions during the nestbound stage), and its potential use in creating more effective breeding populations outweigh the limitations described above. Due to the difficulty of observing red pandas in the wild (Johnson et al. in press; Johnson pers. comm.) captive populations are the most feasible locality for studies of this nature. Thus, information about red panda reproductive behavior that is gleaned from captive research is a viable beginning.

Bearing in mind the limitations outlined above, conclusions can be drawn in terms of scent-marking and maternal care behavior in captive red pandas. Comparative research has shown that much of the variation in carnivore life history characteristics and

behavior can be explained by differences in social structure and feeding strategy (Bekoff et al. 1984; Ewer 1973; Gittleman 1988b). Thus it is useful to discuss red panda scent marking and maternal care behavior in terms of these two parameters.

B. Social structure and feeding strategy - their effects on scent-marking:

As mentioned previously, the bulk of the red pandas' diet consists of bamboo. The pattern of its distribution, as well as the red pandas solitary social structure, may effect the deployment of scent marks within a red pandas range. Resource patterns (e.g., distribution of food or conspecifics) have been shown in other carnivores to have an impact on the distribution of scent-marks within a territory (Macdonald 1985). Species which feed on widely scattered or patchy resources tend to deploy their marks along trails within their range to protect their resources (e.g., Meles meles, European badger: Kruuk 1978; Lynx rufus, bobcat: Bailey 1974; Suricatta suricata, meerkat: Ewer 1963). The patchy distribution of bamboo, then, may have a similar influence on red panda scent-marking. Within the limitations of an enclosure representing a "territory", the data presented for red pandas show a tendency for marking along trails (also see Keller 1977).

Scent-marking patterns may also be considered in terms of the degree of sociality expressed within a species. Group size tends to influence the placement of marks within a species' home range. Spotted hyenas (Crocuta crocuta), which live in clans of up to 55 members, create distinct borders at the edge of their territory with latrines (group defecation sites) and characteristic anal "pasting sites". These borders are maintained constantly by group border patrols (Gorman and Towbridge 1988; Kruuk 1972). Smaller groups (1 to 9 members) of brown hyenas (Hyaena brunnea) deploy their marks throughout their home range, primarily in areas more frequently traversed. Gorman and Mills (1984) have shown this to be an effective strategy for smaller groups which are unable to effectively maintain border mark stations. Intruders, after passing into a brown hyaenas territory, tend to encounter a territory owners' scent-mark within only a few hundred meters.

The most recent indications from data collected in the field support the contention that red pandas are solitary outside the breeding season (Johnson et al. in press; Schaller et al. 1985). Thus, an effective means of scent deployment for a solitary species such as the red panda would be to mark trails traveled most frequently. Intruders will be likely to encounter the marks, and time saved from not having to maintain

territorial borders can be used for activities such as foraging. This pathway-dominated marking pattern has been reported for several solitary carnivore species (see Macdonald 1985 for review) and may occur in the red panda.

Several additional effects of a primarily solitary lifestyle can be seen in the form and function of red panda scent-marking observed in this study. One of these effects was demonstrated in a comparative study between an essentially solitary canid, the maned wolf (Chrysocyon brachyurus), and a social canid, the bushdog (Speothus venaticus); Kleiman (1972) reported distinct differences in their communication mechanisms. The social bushdog utilized signals of a much shorter range (e.g., squeak vocalizations, submissive postures), conversely the maned wolf relied on much longer range signals (e.g., barks, conspicuous threat displays). These social differences were also evident in the two canids manner of defecation; the bushdog defecated (apparently) randomly, whereas the maned wolf defecated site-specifically and tended to urinate over the feces. Kleiman postulated the maned wolves method of scent-dispersal, localized mark sites, made the information more readily available to conspecifics. Differences between the species in terms of olfactory investigation were not addressed in Kleiman's study.

Therefore, whether or not the bushdogs method of defecation was less effective than the maned wolves in communicating a signal was not apparent. The study does, however, point out how more solitary species tend to rely more heavily on communication systems capable of bridging distances in time and space. The predominance, then, of scent-marking in the red pandas communication repertoire is justifiable. This system allows messages to be sent and received over long periods of time without requiring direct contact between individuals. The dense vegetation which red pandas inhabit in the wild requires the marks to be placed conspicuously, elevated on rocks and logs found along main travel routes, all trends which are commonly observed in other carnivores (Gorman and Trowbridge 1988; Macdonald 1985). This insures that the scent-marks will be encountered by others in the range and may facilitate odor dispersal (Peters and Mech 1975).

As has been shown in most carnivores, scent-marking is closely related, functionally, to reproduction. Levels of scent-marking behavior tend to rise during courtship and breeding (see Macdonald 1985 for review). Various studies have outlined the potential information that is available upon investigation of scent-marks. This includes individual

recognition (Gorman 1976; Rasa 1973), temporal information (Leyhausen and Wolff 1959; Rasa 1973), and reproductive state (Doty and Dunbar 1974). For a solitary species such as the red panda, the increase in marking frequency may facilitate encounters of another individuals scent-mark and the information potentially gained from the mark could be used in the search for a mate. Thus, increased marking frequency during the breeding season may raise an individuals' chance of a breeding encounter. In support of this, following trails through the use of scent-marks has been demonstrated in other carnivore species (Eaton 1970; Frame and Frame 1981).

Higher frequencies of marking often occur during encounters between unfamiliar individuals (e.g., during courtship in solitary species). This may perhaps reflect aggressive motivation which is redirected to increased marking rates (Biben 1982; Ralls 1971; Rasa 1973). The high levels of scent-marking exhibited during the initial introduction between the male and female in enclosure #3 may thus reflect the pattern of behavior during an initial encounter. It is predicted that as familiarity between individuals increases, levels of scent-marking in red pandas will most likely be lower (see Porton 1983). This relationship with familiarity may help explain the low levels of marking

behavior in the other two enclosures. The pair in enclosure #2 had shared the area for six years, while the pair in #4 had shared their enclosure for two years.

Sharing sites and preferentially sniffing sites marked by the opposite sex seem to be two mechanisms which would permit effective assessment and recognition among individuals of predominantly solitary species such as the red panda. This idea follows Gosling's (1982) concept of "scent-matching", in which marks previously investigated are matched with any encountered individuals' scent. During breeding encounters it would be to the advantage of both individuals to preferentially investigate sites marked by the opposite sex. In this way the assessment process would be effective. Due to the constraints of the captive setting (e.g., social groups other than male/female pairs were unavailable), it was not possible to determine if the preferential olfactory investigation was directed to marks of members of the opposite sex or more broadly to marks of "non-self" individuals. Regardless, time is potentially saved by not investigating one's own scent-mark. The increase in interaction due to site sharing and sex-specific olfactory investigation may additionally be required for establishing pair bonds (Porton 1983; Rothman and

Mech 1979), albeit temporary ones, in the red panda.

C. Social structure and feeding strategy - their effects on maternal care and neonatal development:

Due to the small sample size (a singleton cub), and the generally descriptive nature of the results, conclusions drawn with respect to maternal care and neonatal development in the red panda are necessarily speculative. With consideration of these limitations, some conclusions may still be drawn concerning red panda social structure and feeding strategy and their influence on maternal care. A central theme which seems to characterize the mother-infant relationship within this species is the energetic constraint placed upon the female which subsequently has an effect on her offspring. This constraint stems from several sources, one of which is the red pandas' maternally based parental care system.

Variation in the number of individuals providing care for the young generally affects neonatal characteristics and perhaps survival. For example, in coyotes (Canis latrans), golden jackals (Canis aureus), and blackbacked jackals (Canis mesomelas), there is a positive correlation between the number of helpers (nonbreeding individuals which aid in caring for litters) in a group and pup survival (Bekoff and Wells 1982; Moehlman 1979). Specific causal factors for the

differential survival are unknown, yet several hypotheses (e.g. increase in defence from predators, increase in provisioning) have been cited (Bekoff and Wells 1986; Moehlman 1987; for review see Gittleman 1985). Regardless of the causal factors, the positive relationship between the number of helpers and offspring survival underlines the impact that an increase or decrease in parental (energy) investment can have on variables such as litter survival. Thus, the energetic investment of a single mother, such as the red panda, may be more constrained than in biparental or communal species.

This energy differential has been further demonstrated in carnivores, in that maternal species produce lighter litters with slower growth rates than do biparental or communal species (Gittleman 1985; Gittleman and Oftedal 1987). In addition to the constraints due to variation in parental care, there are ones inherent in maternal care systems as well. Variables relating to variation in maternal investment (as expressed by pre-weaning litter growth rates) have been outlined in a recent comparative review of carnivore lactation (Gittleman and Oftedal 1987). The review shows further constraints appear to be placed on the abilities of red pandas to transfer energy (via milk) to the young due to feeding strategies based upon

poor quality food. More broadly, herbivorous species (including the folivorous red pandas) showed litter growth rates which were significantly slower than carnivorous or omnivorous members of the order. As growth prior to weaning is dependant upon female lactation performance, variability in milk yield and/or composition is a primary factor in variable litter growth among carnivores (Gittleman and Oftedal 1987).

Further comparison by Gittleman and Oftedal dealt with predicted milk energy outputs at peak lactation for several carnivore species. The predicted output for the red panda was demonstrated to be quite low (0.37 $MJ.kg^{-0.75}$), in comparison with, for example, a value of 0.67 $MJ.kg^{-0.75}$ for the domestic cat and 0.86 $MJ.kg^{-0.75}$ for the raccoon (Procyon lotor). Most carnivores exhibited predicted values between 0.6 and 0.9 $MJ.kg^{-0.75}.d^{-1}$. The authors suggest that the low value predicted for red pandas may be a reflection of the poor quality diet of bamboo (as quantified for the giant panda by Dierenfeld et al. 1982), and its subsequent effect on milk production. Given, then, that the effect of a poor quality diet reduces the energy available through lactation, several facets of maternal care and neonatal development in this species appear to be affected, as demonstrated by this study.

1. Slow litter growth rate -

In the first 30 days after birth, neonatal growth rate for the cub under observation was slower than weight gain rates previously reported for red pandas (7-20 grams/day: see Roberts and Gittleman 1984 for review). After supplemental feeding was initiated, the rate of weight gain reached, and subsequently surpassed the 7-20g/day "norm". This differential growth rate as a result of variation in feeding regimes has been shown in other mammals (e.g., canids: Barnum et al. 1979; ungulates: Robbins et al. 1981) Thus, these results are consistant with and support the contention that milk quality and/or quality is a limiting factor for growth rate in carnivores.

2. Change in nest attendance -

As mentioned previously, pre-weaning growth rates are entirely dependant upon maternal energetic input via milk. As development continues, the energetic demands faced by the mother must necessarily increase (Gittleman 1988a; Gittleman and Oftedal 1987). Compensation for this increased demand may be exhibited by shifts in the maternal time budget (Gittleman and Thompson 1988), for instance by increasing total food intake above non-reproductive rates [e.g. 130% increase, white-footed mouse (Peromyscus leucopus): Millar 1978; 66-111% increase,

cotton rats (Sigmodon hispidus): Mattingley and M^{c}lure 1982; 149% increase, fox-squirrel (Sciurus niger): Havera 1979; for review, see Gittleman 1988a]. The red panda has been shown to significantly increase the duration of feeding bouts during the lactation period, with total food intake increasing to 200% (Gittleman 1988a). Although change in feeding duration taking place within the lactation period was not detected by Gittleman's study, I would suggest that the decline in maternal nest attendance observed in the current study may partially be a reflection of incremental shifts toward longer periods of feeding.

3. Low incidence of play -

Time allocated for play in various mammals has been cited to range from 0-50% of a juvenile's day (review in Fagen 1981). Based on the few bouts observed in the red panda, much less than 1% of the neonate's activity was spent playing. Energetic constraints may have again played a role in the low incidence of play behavior in this species. In a recent review of precocity and play behavior, Burghardt (1988) presents a hypothesis which helps explain much of the variation observed in the degree of play among species. The hypothesis, termed the Surplus Resource Theory, is based on three premises, one of which is that the amount of energy available for allocation to play is

variable among species due to variation in metabolic rates. As a carnivore species possessing one of the lowest basal metabolic rates within the order (McNab 1988), the red panda would certainly be expected to follow many of the predictions Burghardt outlines from his theory. For example:

1. "Play should be very sensitive to nutritional and thermal needs."
2. "Birds and mammals with very low rates of metabolism should play less than those with higher metabolic rates."
3. "Play should peak after neonates are less dependant on parents for food, warmth, and so on. Thus, precocial birds and mammals show play earlier than altricial species."

Each of these predictions essentially describes what is observed in the red panda. As a folivorous species with an extremely low rate of metabolism, the red panda seems to have limited energy to allocate to play behavior, especially during the nestbound stage.

D. Future research goals -

Within both the scent-marking and maternal care studies, there remain several questions requiring further research. In terms of scent-marking in red pandas:

1. Testing for discriminatory ability in both

sexes. This would require some means of obtaining scent-mark samples which could then be presented to various individuals. Previous unsuccessful attempts toward this end were made, however, with further trials elicitation of marking on some removable substrate may be possible. Once the samples were obtained, tests including discrimination between the sexes, individuals and, unfamiliar species could be performed.

2. Long term analysis of site preferences, shared sites, and olfactory preferences. A study encompassing more than one breeding season could indicate if these paramenters remained consistant year round or from one breeding season to the next.

In terms of maternal care and neonatal development in red pandas:

1. Redesigned nestboxes. The addition of scales in the floor of the nest would allow for daily weight monitoring in both the female and the cub without disturbance to the nest. This would also allow for pre- and post-suckling weights to be observed, and thus, some measure of milk transfer would be determined. Thermometers inside the nestbox could more accurately assess if female nest attendance is dependant upon temperature. And finally, improved camera lens width, to provide an entire view of the nest so that behavior occuring "off-screen" will be

eliminated. Collection of these data would allow a more direct assessment of the lactational energetics in red pandas (Gittleman and Thompson 1988).

2. 24 hour observation sessions. This would require some means of lighting the nest without adding heat and/or disturbing the female and her litter. 24 hour observation would allow more accurate descriptions to be made in terms of the female time budget and of development in cub behavior. Perhaps some of the low frequency behaviors observed in this study (e.g., nursing, play), were primarily nocturnal events and thus were missed.

3. Milk sample analysis. Many of the conclusions presented in this study were based on the premise of poor quality milk and its low energy content. Thus, milk samples and their content analysis are required to substantiate these comments.

While some of these goals will be more difficult than others to achieve, I believe that all are necessary if a more detailed and clear picture of red panda reproductive biology is to be obtained. This study has offered some conclusions which can at best be considered speculative, but more positively, has in doing so, provided some insight into the behavioral factors characteristic of red panda scent-marking, maternal care and neonatal development.

LIST OF REFERENCES
CHAPTER IV

Bailey, T.N. 1974. Social organization in a bobcat population. J. Wildl. Mgmnt., 38, 435-446.

Barnum, D.A., Green, J.S., Flinders, J.T., and Gates, N.L. 1979. Nutritional levels and growth rates of hand-reared coyote pups. J. Mammal., 60, 820-823.

Bekoff, M., Daniels, T.J., and Gittleman, J.L. 1984. Life history patterns and the comparative social ecology of carnivores. Annu. Rev. Ecol. Syst., 15. 191-232.

Bekoff, M. and Wells, M.C. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use, and resource defence. Z. Tierpsychol., 60, 281-305.

Bekoff M. and Wells, M.C. 1986. Social ecology and behavior of coyotes. Advances in Study of Behavior, 16, 251-338.

Biben, M. 1982. Urine-marking during agonistic encounters in the bush dog (Speothos venaticus). Zoo Biol., 6, 359-362.

Burghardt, G.M. 1975. Behavioral research on common animals in small zoos. In: Research in Zoos and Aquariums (Eds. National Academy of Sciences), Washington, D.C.: National Academy of Sciences.

Burghardt, G.M. 1988. Precocial behavior, play and the ectotherm-endotherm transition: profound reorganization or superficial adaptation? In: Handbook of Behavioral Neurobiology, Vol. 9 (Ed. E.M. Bass), pp. 107-148. Nwe York and London: Plenum Press.

Dierenfeld, E.S., Hintz, H.F., Robertson, J.B., VanSoest, P.J. and Oftedal, O.T. 1982 Utilization of bamboo by the giant panda. J. Nutr., 112, 636-641.

Doty, R.L. and Dunbar, I.F. 1975. Attraction of beagles to conspecific urine, vaginal and anal soc secretion odours. Physiol. Behav., 12, 825-833.

Eaton, R.L. 1970. Group interactions, spacing and territoriality in cheetahs. Z. Tierpsychol., 27, 481-491.

Eisenberg J.F. and Kleiman, D.G. 1977. The usefulness of behavior studies in developing captive breeding programms for mammals. Int. Zoo Yb., 17, 81-89.

Ewer, R.F. 1963. A note on the suckling behavior of the viverrid, Suricatta suricata (Schreber). Anim. Behav., 11, 599-601.

Ewer, R.F. 1973. The Carnivores. Ithaca, New York: Cornell Univ. Press.

Fagen, R. 1981. Animal Play Behavior. New York: Oxford Univ. Press.

Frame, G.W. and Frame, L.H. 1981. Swift and Enduring: Cheetahs and Wild Dogs of the Serengeti. New York: Dutton.

Gittleman, J.L. 1985. Functions of communal care in mammals. In: Evolution: Essays in Honour of John Maynard Smith (Eds. P.J. Greenwood, P.H. Harvey and M. Slatkin), pp. 187-205. Cambridge: Cambridge Univ. Press.

Gittleman, J.L. 1988a. Behavioral energetics of lactation in a herbivorous carnivore, the red panda (Ailurus fulgens). Ethology (in press).

Gittleman, J.L. 1988b. Carnivore Behavior, Ecology and Evolution. Ithaca, New York: Cornell Univ. Press (in press).

Gittleman J.L. and Oftedal, O.T. 1977. Comparative growth and lactation energetics in carnivores. Symp. Zool. Soc. Lond., 57, 41-77.

Gittleman J.L. and Thompson, S.D. 1988. Energy allocation in mammalian reproduction. Amer. Zool. (in press).

Gorman, M.L. 1976. A mechanism for individual recognition by odour in Herpestes auropunctatus (Carnivora: Viverridae). Anim. Behav., 24, 141-145.

Gorman, M.L. and Mills, M.G.L. 1984. Scent marking strategies in hyaenas (Mammalia). J. Zool. Lond., 202, 535-547.

Gorman, M.L. and Trowbridge, B.J. 1988. The role of odor in the social lives of carnivores. In: Carnivore Behavior, Ecology, and Evolution. (Ed. J.L. Gittleman), Ithaca: Cornell Univ. Press.

Gosling, L.M. 1982. A reassessment of the function of scent-marking territories. Z. Tierpsychol., 60, 89-118.

Havera, S.P. 1979. Energy and nutrient cost of lactation in fox squirrels. J. Wildl. Mgmt. 43, 958-965.

Johnson, K.G., Schaller, G.B., and Jinchu, H. (in press). Comparative behavior of red and giant pandas in the Wolong Reserve, China. J. Mammal.

Jordan R.H. and Burghardt, G.M. 1986. Employing an ethogram to detect reactivity of black bears (Ursus americanus) to the presence of humans. Ethology, 73, 89-115.

Keller, R. 1977. Beitrag zur ethologie des kleinan Pandas (Ailurus fulgens, Cuvier, 1825). Unpublished Ph D. dissertation, Unirsity of Zurich, Switzerland.

Kleiman, D.G. 1972. Social behavior of the maned wolf (Chrysocyon brachyurus) and bush dog (Speothos venaticus): a study in contrast. J. Mammal., 53,791-806.

Kruuk, H. 1972. The Spotted Hyaena, a Study of Predation and Social Behavior. Chicago: Univ. of Chicago Press.

Kruuk, H. 1978. Spacial organization and territorial behaviour of the European badger Meles meles. J. Zool., 184, 1-19.

Leyhausen,P. and Wolff, R. 1959. Das Revier einer Hauskatz. Z. Tierpsychol., 16, 666-670.

McNab, B.K. 1988. Rate of metabolism, body size, and food habits in the order Carnivora. In: Carnivore Behavior, Ecology and Evolution (Ed. J.L. Gittleman), Ithaca, New York: Cornell Univ. Press.

Macdonald, D.W. 1985. The carnivores: order Carnivora. In: Social Odours in Mammals (Eds. R.E. Brown and D.W. Macdonald), pp. 619-722. Oxford: Clarendon Press.

Markowitz, H. 1975. Analysis and control of behavior in the zoo. In: Research in Zoos and Aquariums (Ed. National Academy of Sciences), Washington, D.C: National Academy of Sciences.

Mattingley, D.K. and McClure, P.A. 1982. Energetics of reproduction in large-littered cotton rats. Ecology, 63, 183-195.

Millar, J.S. 1978. Energetics of reproduction in Peromyscus leucopus: the cost of lactation. Ecology, 59, 1055-1061.

Moehlman, P.D. 1979. Jackal helpers and pup survival. Nature, Lond., 277,382-383.

Moehlman, P.D. 1987. Social organization in jackals. Am. Scient., 75, 366-375.

Moran, G. and Sorensen, L. 1986. Scent-marking behavior in a captive group of meerkats (Suricatta suricata). J. Mammal., 67, 120-132.

Peters, R.P. and Mech, L.D. 1975. Scent-marking in wolves. Am. Scient., 63, 628-637.

Porton, I. 1983. Bush dog urine-marking: its role in pair formation and maintenance. Anim. Behav., 31, 1061-1069.

Ralls, K. 1971. Mammalian scent-marking. Science, 171, 443-449.

Rasa, O.A.E. 1973. Marking behaviour and its significance in the African dwarf mongoose, Helogale undulata rufula. Z. Tierpsychol., 32, 449-488.

Roberts, M.S. 1981. The reproductive biology of the red panda, Ailurus fulgens, in captivity. Unpublished M.Sc. thesis, University of Maryland.

Roberts, M.S. and Gittleman, J.L. 1984. Ailurus fulgens. Mammalian Species Account No. 222, 1-8.

Robbins, C.T., Podbielancik-Norman, R.S., Wilson, D.L., and Mould, E.D. 1981. Growth and nutrient consumption of elk calves compared to other ungulate species. J. Wildl. Mgmt. 45, 172-186.

Rothman, R.J. and Mech, L.D. 1979. Scent-marking in lone wolves and newly formed pairs. Anim. Behav., 97, 94-117.

Schaller, G.B., Jinchu, H., Wenshi, P. and Jing, Z. 1985. The Giant Pandas of Wolong. Chicago: Univ. of Chicago Press.

VITA

Greta K. Conover was born in Athens, Ohio on June 23, 1963. She attended elementary schools in that city and graduated from Athens High School in June 1981. The following September she entered Rollins College in Winter Park, Florida, and in June 1985 she received a Bachelor of Arts degree in Biology. In the fall of 1985 she accepted a teaching assistantship at The University of Tennessee, Knoxville, and received her Master of Science degree in Life Sciences in August 1988.