MONTANA STATE UNIVERSITY

Effects of helping behaviors on coyote packs in Yellowstone National Park, Wyoming
by Kezha Guittard Hatier

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Biological Sciences
Montana State University
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Abstract:
Helping behaviors, during the denning season, were studied for twelve coyote packs (Canis latrans) in Yellowstone National Park ,Wyoming. Of 14 helpers 12 (86%) were known to be related to one or both of the alpha pair they helped. Observations were made from the end of April until the end of July during the summers of 1992 and 1993. The den site was the area of focus, and only one coyote was observed at a time. Summers were divided into three biologically defined periods; the beginning and end of each period was determined by the temporally changing needs of the pups. Objectives were to compare the differences in helping behaviors between the adults in a pack, to determine if there was a difference in behaviors among adults from period to period, to determine if the age of the beta helpers and the size of the litter influenced the amount of time they spent helping, to determine if the alpha pair benefited from the presence of the beta helpers, and to determine if the pups benefited from the presence of the betas. All alpha females were alone more than all alpha males during period one, and they played more with the pups during period three. Alpha females with betas socialized with the young more during periods two and three, and regurgitated more with the young during period three than did alpha females without betas. Alpha males without betas howled more during period two than did alpha males without betas. Alpha females with betas were present at the den, and alone at the den more than alpha males with betas during the first period. Beta females were present at the den more than were beta males during period one, and alone at the den more than were beta males during period three. Beta males were alert at the den more than were beta females during period three. There was no difference in the amount of time all alpha females and all alpha males were present from period to period. Beta females spent more time present during period one, less time present during period two , and the least time present during period three. The beta males were present at the den less during period one than during period two, and the least during period three. Alpha and beta females were alone the most during period one, the least during period two, and less than period one during period two. Beta males were alone the den the most during period two, less during period one, and the least during period three. The amount of time betas spent helping was not influenced by their age or the number of young in the litter. However only one beta was older than two years. There was a positive correlation between the size of the pack and the initial litter size, and between the number of provisionings and the litter size. There was also a positive correlation between the number of feedings to the pups from the alpha female and the size of the litter. There was no correlation between the number of betas in a pack and the amount of time the alpha pair spent resting. Pups in larger packs were left alone less, and fed more than pups in smaller packs. There was a negative correlation between the size of the pack and the survival of the pups until August. However, the pups were hit heavily with Parvo virus one year, and this undoubtedly skewed the results.

EFFECTS OF HELPING BEHAVIORS ON COYOTE PACKS

IN

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by

Kezha Guittard Hatier

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Kezha Guittard Hatier

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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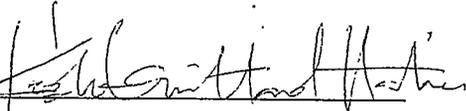
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ABSTRACT

Helping behaviors, during the denning season, were studied for twelve coyote packs (*Canis latrans*) in Yellowstone National Park ,Wyoming. Of 14 helpers 12 (86%) were known to be related to one or both of the alpha pair they helped. Observations were made from the end of April until the end of July during the summers of 1992 and 1993. The den site was the area of focus, and only one coyote was observed at a time. Summers were divided into three biologically defined periods; the beginning and end of each period was determined by the temporally changing needs of the pups. Objectives were to compare the differences in helping behaviors between the adults in a pack, to determine if there was a difference in behaviors among adults from period to period, to determine if the age of the beta helpers and the size of the litter influenced the amount of time they spent helping, to determine if the alpha pair benefited from the presence of the beta helpers, and to determine if the pups benefited from the presence of the betas. All alpha females were alone more than all alpha males during period one, and they played more with the pups during period three. Alpha females with betas socialized with the young more during periods two and three, and regurgitated more with the young during period three than did alpha females without betas. Alpha males without betas howled more during period two than did alpha males without betas. Alpha females with betas were present at the den, and alone at the den more than alpha males with betas during the first period. Beta females were present at the den more than were beta males during period one, and alone at the den more than were beta males during period three. Beta males were alert at the den more than were beta females during period three. There was no difference in the amount of time all alpha females and all alpha males were present from period to period. Beta females spent more time present during period one, less time present during period two , and the least time present during period three. The beta males were present at the den less during period one than during period two, and the least during period three. Alpha and beta females were alone the most during period one, the least during period two, and less than period one during period two. Beta males were alone the den the most during period two, less during period one, and the least during period three. The amount of time betas spent helping was not influenced by their age or the number of young in the litter. However only one beta was older than two years. There was a positive correlation between the size of the pack and the initial litter size, and between the number of provisionings and the litter size. There was also a positive correlation between the number of feedings to the pups from the alpha female and the size of the litter. There was no correlation between the number of betas in a pack and the amount of time the alpha pair spent resting. Pups in larger packs were left alone less, and fed more than pups in smaller packs. There was a negative correlation between the size of the pack and the survival of the pups until August. However, the pups were hit heavily with Parvo virus one year, and this undoubtedly skewed the results.

INTRODUCTION

Among the major factors influencing the social organization of a population are its mating systems, its spacing patterns, and its feeding ecology (Moehlman 1983). Monogamy is a mating system rare in mammals (Moehlman 1983). It has been documented in many canids, but not felids. Canid males feed the young with regurgitated food (Wittenberger and Tilson 1980) and help to rear and to protect their young, whereas felid males do not. Two ways monogamous mammals may care for their young are biparentally, and communally. Biparental care is defined as the establishment of monogamy between a male and a female, and parental duties are divided among each (Gittleman 1985). In some families of mammals, communal care includes both biparental care and alloparental helpers to share with the duties of rearing the young. These helpers, of either sex, serve to guard, and to feed the current offspring (Gittleman 1985). Alloparental helpers do not mate, but expend time and energy to rear young that are not their own (Malcolm and Marten 1981). The degree of relatedness between such helpers and breeders, (consequently, between helpers and young) is one of the primary factors influencing non-parental aid or "helping behavior" (Owens and Owens 1984). Thus, helping may have evolved via kin selection, the process by which a trait is favored because of its beneficial effects on relatives, such as siblings or cousins (Maynard Smith 1964).

Spacing patterns also can affect the social organization of a population. If individuals are territorial, and unoccupied territories are rare, the young may have to travel great distances before they can settle. If the young remain on their parents territory, they may increase their rate of survival which also would benefit the parents (Selander 1964). However, with each member added to a family group, there must be a high enough food base to support all. Von Schantz (1984) hypothesized that the evolution of kinship groups can be induced by a temporary resource surplus within the territories. Helping can be either direct or indirect. Direct helping occurs only in response to the presence of the young, and includes such activities as feeding, carrying, grooming, playing with, and protecting the young (Gittleman 1985). Indirect helping might include defense of a territory or feeding a breeding female while she is pregnant. There are many benefits and some costs that have been attributed to communal breeding and to different forms of helping. The pack benefits from greater coordination of group movements, and by sharing of information. The breeders may benefit from the non-breeders' help in the care and rearing of their current offspring (Emlen 1978). The acceptance of genetically related helpers may ensure that the young reared in the territory after the breeders' death are related to them (Brown 1974, Woolfenden and Fitzpatrick 1978). Furthermore, a larger pack helps to divide the labor of caring for offspring. With a shortage of available territories helpers benefit by staying on their natal territory; they gain more easily food, a relatively safe environment, and experience. The breeders allow them to remain because of a surplus of resources,

and because of the benefits to the breeders from helping. Finally, current offspring can receive a higher rate of food intake, and more protection from predators.

In order to maintain helping behaviors in a population, the benefits to breeders and to helpers should exceed costs when one or more helpers remain on the territory, and whatever costs might be experienced by the helper in not breeding (Kinnaird and Grant 1982). Among the costs to all members of a pack, attributed to the presence of helpers, are increased competition, increased transmission of disease or ectoparasites, increased conspicuousness to predators, and increased aggression (Gittleman 1985). Helpers alone withstand the cost of delaying reproduction.

Among species that engage in a variety of group-level activities, decisions about grouping patterns are likely to be highly complex (Packer 1990). Bertram (1978) found that the presence of subordinate non-breeding adults (betas) within groups of genetically related individuals appears to be widespread in carnivores. In addition, species that have communal care tend to live in small (3-10 individuals), relatively stable groups in well-defended territories.

In Yellowstone National Park coyote (*Canis latrans*) packs in the northern range are made up of either the dominant and breeding alpha pair and of the subordinate nonbreeding betas, or of the alpha pair only. Only a structured pack, never a lone coyote or unstructured group, was observed, during this study, to hold a territory. Most of the packs studied had beta helpers. Coyote pups are born at the end of April, or the beginning of May (Bekoff and Wells 1981). Their first two weeks are spent entirely in the den. They are helpless, toothless, hairless and blind (Gier 1975)

for about the first ten days, during which they depend completely on the mother for their nourishment and for their protection, and on their newborn siblings and their mother for heat. They cannot use their teeth until about six weeks of age (Gier 1975), so milk continues to be their staple diet until their teeth can be used to tear meat apart. The pups begin to eat regurgitated food about the beginning of June and hard food at the end of June. They are not very mobile for the first few weeks, and usually can run quickly by the middle or end of June. By the end of July, they rarely use the den, but they do have rendezvous sites near the most recent den, and often travel with the adults. If the young disperse from their natal territories, they do so from September through January.

In winter, coyotes may hunt alone, or in packs when they try to kill large prey. In which case, the alpha male usually takes down the prey before the other pack members help with the final kill (Gese and Grothe 1995). In the summer, however, when the pups are growing, Yellowstone coyotes seem to hunt alone. In this case the prey they take is fairly small and can be handled by one adult. For example, during the denning season the coyotes have an ample supply of Uinta ground squirrels (*Spermophilus armatus*), elk calves (*Cervus elaphus*), voles (*Microtus* spp.), pronghorn fawns (*Antilocapra americana*), and pocket gophers (*Thomomys talpoides*).

Winter pack size decreased slightly in Yellowstone Park during the denning season, and the boundaries of the territories were enforced more during the mating and early denning season than during the beginning of winter (Crabtree 1989). There was an even sex ratio of beta helpers. Most of the betas of a known age

were one to two years old, and were the offspring of the alpha pair they helped.

The northern range has much open habitat which makes observing the coyote behavior from a distance accurate. Coyotes in Yellowstone Park are, for the most part, monogamous. Because of high population density, and because territories are fixed at about 3-4 square miles, there is little room for territorial change. Consequently, the chance of a dispersing coyote finding unoccupied territory is slim. Yellowstone Park offers the advantage of studying coyotes in an area where they are relatively undisturbed. To my knowledge, no study has focused on the contributions of coyote helpers to the pack. Because coyotes are wary, it is difficult to observe coyotes in the wild. This study provided a chance to examine the behavior of coyotes during their denning season in natural surroundings. Furthermore, cohesive family groups are found most often in remote areas or locations where coyotes are relatively unpersecuted (McMahan 1975).

My objectives and hypotheses were as follows:

1. Objective: To determine the relationship in social position between adults (one or more years old) in the pack, and their roles in rearing the pups.
Hypothesis: There will be differences in behaviors among the different levels of social class and/or the different sexes.
Null: There will be no difference in behaviors among different levels of social class and/or the different sexes.

2. Objective: To examine the phenology of denning behavior of twelve coyote packs in Blacktail Plateau and Lamar Valley.
Hypothesis: The proportion of time the alphas and the betas are present at the den, and guarding the pups will change as the pups grow.
Null: The proportion of time the alphas and betas are present at the den, and guarding the pups will not change as the pups grow.

3. Objective:To determine whether the amount of time spent by betas on
helping to rear pups is influenced by the age of the betas
and/or by the number of pups in a litter.
Hypothesis:The age of the betas and the size of the litter will affect the amount
of time the betas spend with the pups.
Null:The age of the betas and the size of the litter will not affect the
amount of time the betas spend with the pups.

4. Objective:To determine whether the alpha pair benefit directly from the helping
behaviors of betas.
Hypothesis:The alpha pair will benefit from the presence of betas.
Null:The alpha pair will not benefit from the presence of betas.

5.Objective:To determine whether the presence of betas influences the survival
of the pups.
Hypothesis:The presence of betas will benefit the current pups, by an
increase in their rate of survival, their rate of food intake, and
a decrease in the amount of time they are left alone.
Null:The presence of betas will not benefit the current pups.

STUDY AREA

The two areas of study were in the northern range of Yellowstone National Park in northwest Wyoming (Figure 1 and Figure 2). The first was on the Blacktail Plateau, 16 kilometers east of Mammoth, Wyoming. The second was in Lamar Valley, 40 kilometers east of Mammoth.

Blacktail Plateau is at an elevation of 1920 meters. The average annual temperature ranges from a high of 18 degrees C, to a low of -6 degrees C. The average annual precipitation is 28 centimeters, with an average annual snowfall of 278 centimeters (Dirks 1982). Each territory, of the four packs studied (Deer Creek, Oxbow, Blacktail, and Lava Creek), included rolling grassland hills covered with big sagebrush (*Artemisia tridentata*), Idaho fescue (*Festuca idahoensis*), quaking aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) (Despain 1990). There are either small creeks or ponds in each territory and the Park's Northeast Entrance Road runs across this plateau.

Lamar Valley is at an elevation of 1988 meters. The average annual temperature is a high of 16 degrees C, with an average low of -12 degrees C. The average annual precipitation is 28 centimeters, with 278 centimeters of snowfall annually (Dirks, 1982). The Lamar River flows through the valley and defines a border for three of the four packs' territories (Norris, Druid, and Bison packs); the fourth packs' territory (Soda Butte) is bisected by Soda Butte Creek. The upland slopes of each territory overlook the valley and the flat open grassland of the valley floodplain. The slopes are grown with aspen, lodgepole pine, and Douglas fir, the valley with

lodgepole pine, Douglas fir, Engelmann spruce (*Picea engelmannii*), big sagebrush, and Idaho fescue (Despain 1990). Each territory includes 2-4 km² of mesic floodplain dominated by sedges and an occasional shrub. The Northeast Entrance Road runs across three of the four packs' territories.

The primary mammal fauna on each study site are coyote, grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), mountain lion (*Felis concolor*), badger (*Taxidea taxus*), red fox (*Vulpes vulpes*), weasel (*Mustela frenata*, *M.erminea*), river otter (*Lutra canadensis*), vole (*Microtus* spp.), Uinta ground squirrel (*Spermophilus armatus*), pocket gopher (*Thomomys talpoides*), deer mice (*Peromyscus maniculatus*), muskrat (*Ondatra zibethicus*), bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), elk (*Cervus elaphus*), mule deer (*Odocoileus virginianus*), buffalo (*Bison bison*), and antelope (*Antilocapra americana*).
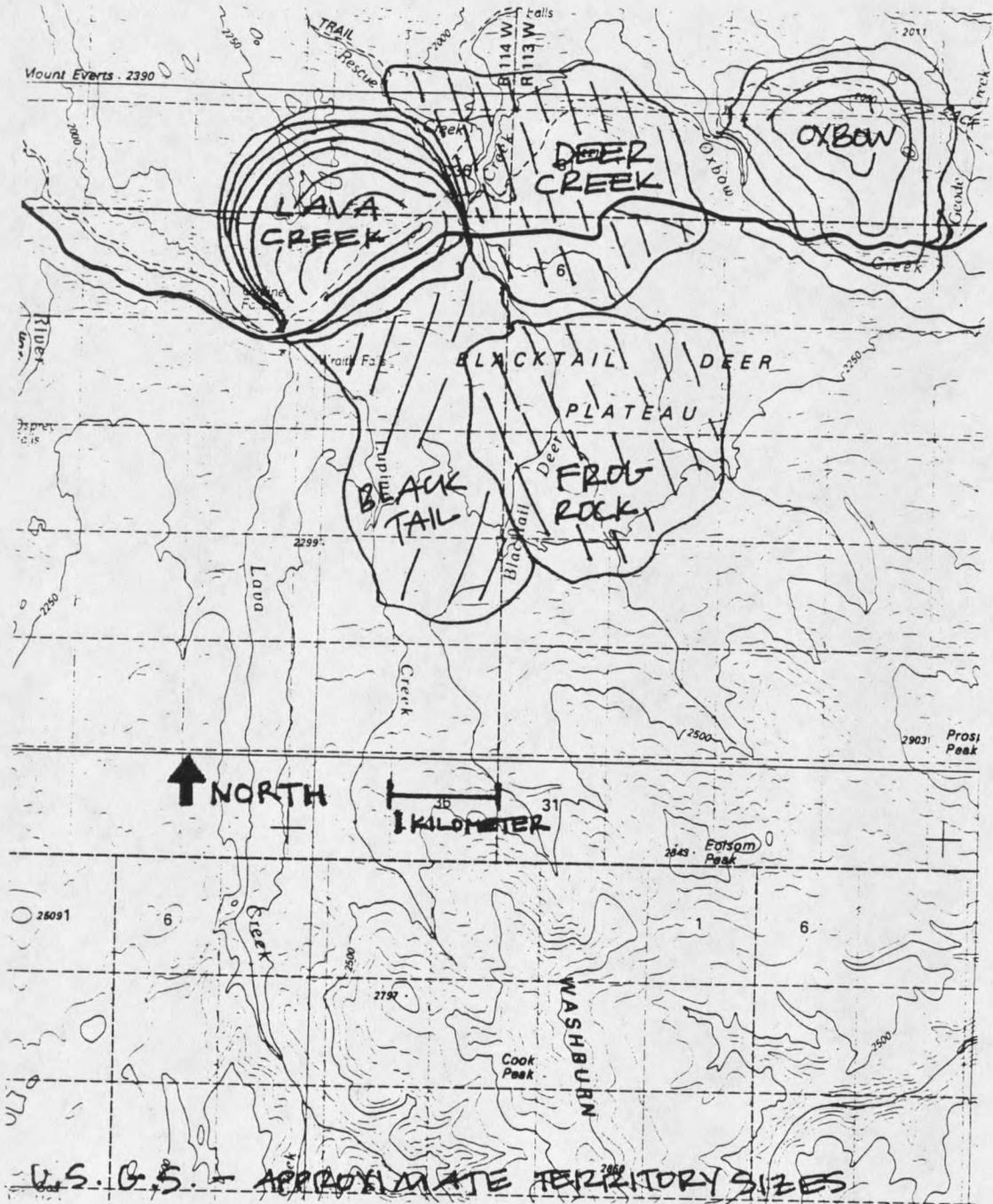
Figure 1. Study area 1 on Blacktail Plateau. Including the territories of the Lava Creek, the Deer Creek, the Blacktail, and the Oxbow coyote packs.
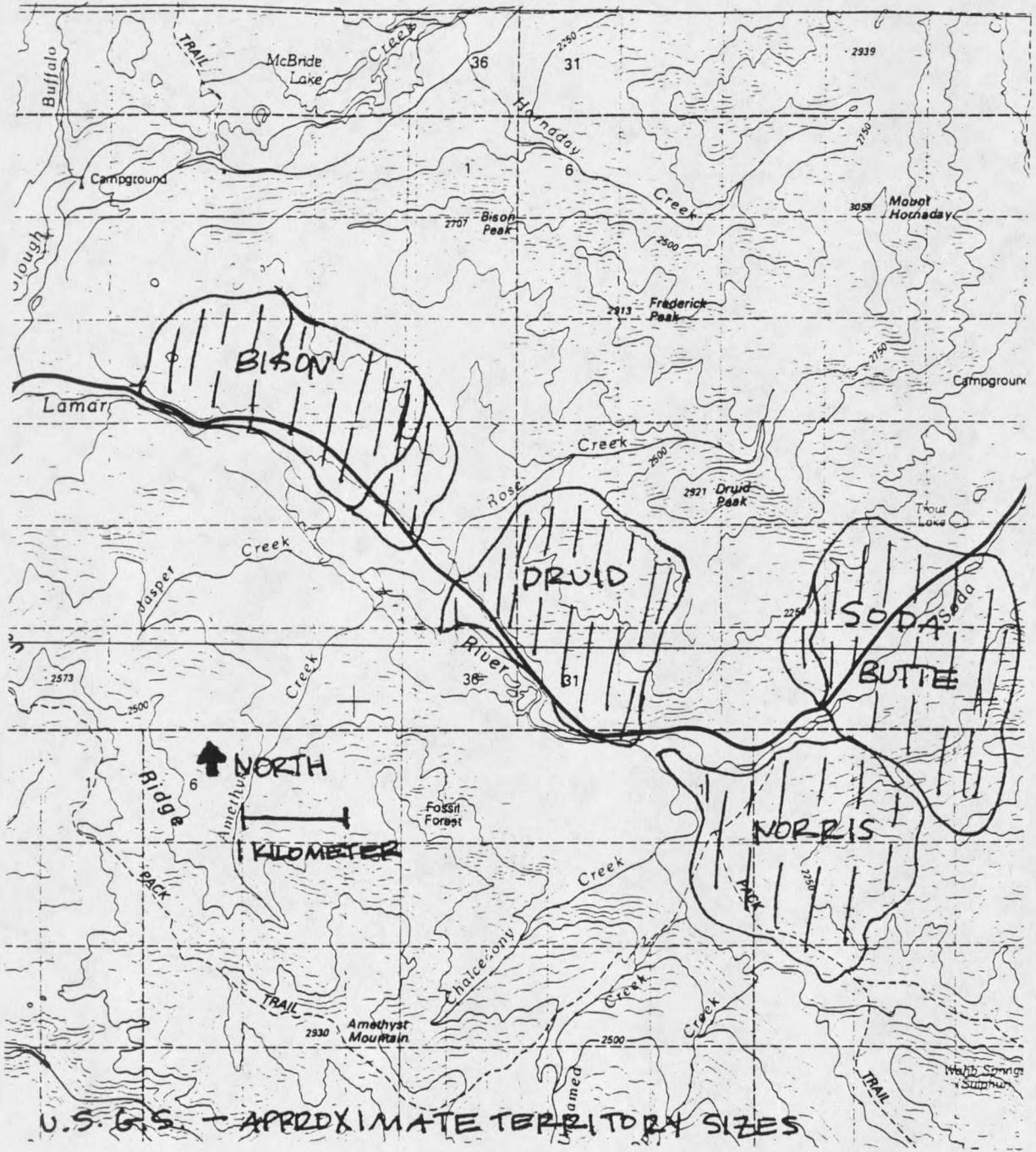
Figure 2. Study area 2 in Lamar Valley. Including the territories of the Bison, the Druid, the Norris, and the Soda Butte packs'.

METHODS

Capture

In the autumns of 1990, 1991, 1992, and 1993 coyotes were live trapped and released with colored ear tags and Telonics radio collars. During June of 1990, 1991, 1992 and 1993 Telonics intraperitoneal radio transmitters, which emit mortality signals triggered by a temperature of 35 degrees C, were implanted into the abdominal cavities of the pups. The collars, implants, and eartags allowed the coyotes to be identified reliably. Those few that were not tagged were identified by their markings.

Observations

. The data were collected from the end of April through July in the summers of 1992 and 1993. Observers sat 200 m or more from the den area of focus. Nikon and Bushnell spotting scopes were used with 15-45x zoom capability. Therefore, it is presumed that the behaviors of the coyotes were observed accurately, without disturbing them. When an adult was farther than 250 m from the den this was considered out of the den area. It was assumed generally that if the adults were more than 250 m away, they were not able to watch the den. Therefore, the data collected were biased towards the minimum amount of time the adults

devoted to activities near the den. Harrison and Gilbert (1985), in their telemetry study on the rates of coyote adults' movements around the den, chose to use a 300 m radius. However, the relevant distance will tend to vary depending on habitat. For example, the Norris pack, studied in Yellowstone National Park, lived in an area with few trees or hills, so it is assumed adults could see the den from 400-500 m.

Radio telemetry was used to find the dens, and to determine if an animal was in the den area when not visible. If a coyote left the den area, then it was recorded as out of the den area and was no longer watched. Contact was recorded as lost if a coyote was being watched and it disappeared, whether in the den area or out. Therefore, again, the presence of the adults at the den represents an underestimate of time present.

In 1992 behaviors were recorded into hand held tape recorders, and later entered into computer. In 1993, a program was developed (Scott Grothe, M.S.U. biology department) to record the behaviors directly into a computer. That summer, the data were recorded in the field into Hewlett Packard HP95 palmtop computers. For both years, the length of time of behaviors categorized as ratios lasted were recorded to the nearest second. However, behaviors such as bringing food, regurgitating, nursing, howling, playing, grooming, and socializing were considered instantaneous; therefore they were analyzed as rates (Table 1). There may be a slight bias increasing the duration of the behaviors. It took six seconds for the behaviors to register in the computer. However, it took the same amount of time for each behavior recorded on every

animal, so this should not influence the data comparisons.

Any given coyote pack was observed for approximately six hours a day, and observations were rotated between morning-afternoon shifts one day, then afternoon-evening shifts the next. Therefore, the data should not be biased towards behaviors happening more at one time of day than another. Maintaining constant number of observational hours for each pack was the objective, but this was precluded sometimes by the coyotes' moving pups to new dens. In some cases, it was not possible to watch a particular den without being too close. Also, since the number of field technicians varied throughout the summer, some weeks it was possible to sample each pack every other day. With fewer observers, there were times when each pack could be sampled only once a week.

Two of eight packs in 1992 had no betas, and two of four in 1993 had no betas. Since some betas were seen on the territory, but never around the den, they were not considered helpers. Therefore some packs had more betas than were registered in the tables and in the figures (See Table 5). The four packs observed in 1993 were of the same eight packs observed in 1992. However, each of the four packs consisted of different adults in 1993 than it did in 1992, therefore they were considered different packs. The years 1992 and 1993 were separated in the analyses. There were three betas that were present during both denning seasons. These overlaps may influence the independence of the samples slightly.

To avoid disturbing the coyotes, if a coyote was present at the den and consistently looked towards the observer, the observation was stopped, or the observer would move to a spot were the coyote did not seem aware of the observers presence. Therefore it is unlikely that the presence of the observer affected the behaviors of the coyotes.

Definitions

The denning season was broken into three biologically defined periods (in order to test the hypotheses mentioned in the Introduction) to which dates were applied: Approximately 20th April-19th May (birth of the pups-beginning of weaning), 20th May - 19th June (end of weaning- beginning to eat regurgitated food), and 20th June - 20th July (end of eating regurgitated food -eating whole prey). Each behavior was analyzed according to these biological periods, enabling a detection of the change in behaviors according to the temporally changing needs of the pups.

The behaviors analyzed are listed in Table 1. They are not mutually exclusive. Some were subdivided for the data entry, but not for the analyses. The rates were determined by calculating the number of counts for each coyote per biological period divided by the number of hours the coyote was present in that period. The means were determined by adding together the percent of time each coyote spent on a given behavior during each period, divided by the number of observation days for that coyote for that period.

Data Analysis

To test part of hypothesis 1 Students t-tests were used with an arcsine data transformation on S.A.S. with the years 1992 and 1993 separated. Behaviors analyzed on the t-test were the percent of time an animal was present at the den, was alone at the den, and was alert at the den. Behaviors categorized as rates were analyzed using S.A.S. with a Wilcoxon nonparametric one-way test. The years 1992 and 1993 were separated when entered into the computer for analysis, but one result was given for the two years. Two social classes were analyzed at a time (for example, alpha males compared with alpha females) for both the Wilcoxon tests and the t-tests, with nine social classes possible: 1. all alpha females, 2. all alpha males, 3. all betas, 4. all alpha females with betas, 5. all alpha males with betas, 6. all alpha females without betas, 7. all alpha males without betas, 8. all beta females, and 9. all beta males.

Table 1. Definitions of the behaviors analyzed from twelve coyote packs on the northern range in Yellowstone National Park.

BEHAVIOR	DEFINITION
Ratios	
PRESENT	The presence of an adult at the den, whether alone or with another adult.
ALONE	The adult at the den with no other adults present.
ALERT	This includes stand scanning, lying with head up, sit scanning, and the sphinx position.
GUARDING	From perspective of the pups; one or more adult at the den. Same as "present".
RESTING	This includes any adult, in the den area, lying with head down, or sitting and not scanning.
Rates	
PLAYING	Adults interacting with the pups in play behavior.
SOCIALIZING	This includes nuzzling, nudging, or growling.
HOWLING	Adults giving a long howl.
ATTENTION	Adults socializing with, playing with, and grooming the pups.
GROOMING	Adults cleaning, licking, or pulling at pups skin.
NURSING	Only by the alpha female
REGURGITATING	An adult bringing regurgitated food to the den.
BRINGING FOOD	An adult bringing whole, dead prey to the den.

Kruskal-Wallis tests were used on MSUstat to test the difference in rates of provisioning the pups among different pack members. Tests run were; the difference between the feedings (i.e. regurgitations and bringing of whole food) to the pups from alpha females with betas, and from all betas combined; the difference between the number of feedings to the pups from alpha males, and the number of feedings and nursings from alpha females in a pack; the difference between the number of feedings to the pups from alpha males with betas, and the number of feedings from the betas in a pack. A Kruskal-Wallis test was used also to test the difference between the number of feedings from the alpha pairs with betas and the number of feedings from the betas in a pack; the difference between the number of feedings and nursings from alpha females with betas, and the number of feedings from the betas; and, the difference between the number of feedings from the alpha males and the number of feedings from the alpha females.

For hypothesis 2 a Kruskal-Wallis rank test on MSUstat was used, to compare the change in amount of time spent present at the den, and alone at the den across periods for alpha females, alpha males, betas of both sex, and alpha females and males both with and without betas. For hypothesis 3 Spearman rank correlations on MSUstat were used to test the age of betas compared with the average percentage of time they spent at the den; to compare the age of the betas with their rates of regurgitations and bringing of food; to compare the rates of attention to the pups from the betas with the number of betas per pack; and to compare the size of the litter with the time the betas spent present at the den.

Spearman rank correlations were run on MSUstat to test hypothesis 4. Tests were run to find the correlation between pack size and initial litter size, and to find if there was a correlation between the number of betas per pack, and the average percentage of time alpha females spent resting at the den. To see if litter size influenced the behaviors of the pack a Spearman rank test was used to find the correlation between; the number of feedings from the alpha pair and betas combined and the size of the litter; and the number of nursings and the size of the litter; the number of feedings from the alpha female and the number of pups in a litter; the number of feedings from the alpha male and the number of pups in a litter; and the percentage of time the alpha pair is present at the den and the number of pups in a litter.

A Spearman rank test was used also to determine if the number of betas per pack influenced the activities of the alpha pair. Tests were run to find correlations on the following: if the percentage of time all alpha males and alpha females were present at the den over the summer correlated with the number of betas they had in their packs; if the rate of nursings of all alpha females correlated with the number of betas in their pack; if the number of feedings by the alpha female correlated with the number of betas in her pack; if the number of feedings from the alpha male correlated with the number of betas per pack; if the number of regurgitations and bringing of food by the betas correlated with the number of betas per pack; and finally, if the amount of attention the pups received correlated with the number of betas per pack.

For hypothesis 5 a Spearman rank correlation was used to determine if the survival of the pups through the year correlated with the number of betas per pack; if the number of betas per pack correlated with the survival of the pups until August; if the mean percentage of time the pups were alone in the summer correlated with the number of betas per pack; if the number of betas in a pack correlated with the number of fleas found on the pups at time of implanting; if the number of regurgitations and food brought to the pups (from all pack members) over the summer correlated with the number of betas; and if the number of pups in a litter correlated with the number of regurgitations and bringing of food from the betas. Finally, a Spearman rank test was used to find if there was a correlation between the size of the pack and the weight of the pups at capture. In order to make weights recorded at different times equal, true weights were compared with weights from coyote pups measured in another study (Bekoff,1978).

The significant alpha value used for all tests is 0.10. If a behavior is not mentioned in the results it had a high p-value (P >0.20). Because of a small sample size, in some tables, I included the mean rates or percentages of certain behaviors. This was done only for those cases where the characteristics of the means supported what had been observed in the field, and where, given a bigger sample size, statistical tests might have proved significant.

RESULTS

Total Observation Time

All den sites were observed for a total of 565.4 hours in 1992, and for 437.2 hours in 1993. The number of hours that each pack was observed varied among packs and years (Table 2).

Table 2. Coyote packs observed; and the number of days, the number of hours, and the years observations took place.

Coyote Packs	Days	Hours	Year
Soda Butte	7	33.0	1992
Norris	21	112.4	1992
Druid	5	32.2	1992
Bison	21	118.3	1992
Blacktail	8	51.0	1992
Deer Creek	17	72.2	1992
Oxbow	23	128.4	1992
Lava Creek	4	17.1	1992
Druid	23	148.0	1993
Deer Creek	7	25.2	1993
Oxbow	26	150.0	1993
Lava Creek	23	114.1	1993
TOTAL	**185**	**1002.6**	

Background of Pup Growth

In Yellowstone National Park coyotes use underground dens only while rearing their pups. Alpha females, and occasionally the alpha male or an adult helper, enter the dens to reach the pups during the denning season (late March-early July). The pups emerged from their dens, both in the Blacktail Plateau and in the Lamar Valley, approximately the middle of May. Table 3 presents a chronology of the biological and behavioral changes observed in the pups throughout the denning season. During these first few months the pups were quite social both with each other and with the adults; acts of dominance and playing were quite common. Because of a need for information of identified betas and pup survival, pups were captured at den sites during the study and before the study was initiated. Table 4 presents the weights of the pups at capture; the presence or absence of fleas at capture; whether or not the pups survived through December; the pups' sex; and the year of the pups' capture.

The packs moved to new dens several times each summer. The natal den usually was on a dry south-facing slope, and was made often from an old badger den or an enlarged ground squirrel hole. Each pack had many dens available per territory and would use them year after year, sometimes alternating years of use.

Table 3. Biological characteristics of denning season, and what events, in relation to the pups, each period entails.

EVENT	PERIOD ONE 19th April-19th May	PERIOD TWO 20th May-19th June	PERIOD THREE 20th June-20th July
PUP DEN EMERGENCE	YES	NO	NO
RISK OF PREDATION FOR PUPS	LOW (pups mostly in den, about 80%)	HIGH (out of den, wobbly)	MEDIUM (out of den, alert)
PRIMARY FOOD FOR PUPS	MILK	REGURGITATED FOOD, SOME HARD FOOD, SOME MILK,	HARD FOOD, SOME REGURGITATED
ENERGETIC DEMAND ON ADULTS FOR PROVISIONING PUPS	HIGH FOR FEMALES (0.22-1.36 kg pup weight)	HIGH FOR ADULTS (1.36-2.7 kg pup weight)	HIGH FOR ALPHAS (>2.7 kg pup weight)
PUP MOVE-MENT FROM DEN WHEN ALONE	LOW (0-6 m)	MEDIUM (0-50 m)	HIGH (0-200+ m)
RISK OF DISEASE FOR PUPS	LOW (passive immune system from mother)	MEDIUM (nurse less, not as many antibodies from mother)	HIGH (no mother's antibodies, none of own)

Table 4. Pups weight at capture; the presence or absence of fleas at capture; the survival status of the pups by December; the sex of pups; the size of packs, and the year of pup capture.

PACK	WEIGHT	FLEAS	STATUS	SEX	PACK#	YEAR
Soda Butte	1.06	no	A	F	5	1990*
Soda Butte	1.09	no	A	M	5	1990*
Soda Butte	1.27	no	A	M	5	1990*
Soda Butte	1.11	no	D?	M	5	1990*
Crystal	1.45	no	D?	F	?	1990*
Crystal	0.99	no	A	M	?	1990*
Crystal	2.72	no	A	M	?	1990*
FossilForest	2.76	no	D?	M	4	1991*
FossilForest	3.18	yes	D?	F	4	1991*
FossilForest	2.80	no	A	M	4	1991*
Bison	1.76	yes	D?	M	5	1991*
Bison	1.64	no	D?	M	5	1991*
Bison	1.59	no	A	M	5	1991*
Bison	1.75	no	A	M	5	1991*
Druid	3.90	no	D?	M	5	1991*
Druid	3.90	no.	A	M	5	1991*
Druid	4.02	no	A	M	5	1991*
Druid	4.17	no	A	M	5	1991*
Druid	2.10	no	A	F	5	1991*
Amethyst	1.90	no	A	F	?	1991*
Amethyst	2.27	no	A	F	?	1991*
Amethyst	1.80	no	A	M	?	1991*
Amethyst	1.80	no	A	F	?	1991*
Frog Rock	2.14	no	A	M	6	1991*
Bison	3.40	no	D?	F	5	1992
Bison	3.18	no	D?	F	5	1992
Bison	1.36	no	A.	F	5	1992
Bison	1.36	no	A	M	5	1992
FossilForest	5.00	yes	DP	M	5	1992*
Norris	2.27	no	D?	F	4	1992
Norris	2.27	no	A	F	4	1992
Norris	2.50	no	A	M	4	1992
Deer Creek	3.18	yes	DP	M	4	1992
Deer Creek	3.18	no	DP	F	4	1992
Soda Butte	3.18	yes	DP	F	3	1992
Soda Butte	2.95	yes	A	F	3	1992
Soda Butte	3.18	no	A	M	3	1992
Lava Creek	2.35	yes	D?	M	4	1992
Lava Creek	2.27	yes	D?	F	4	1992
Lava Creek	2.95	yes	D?	M	4	1992
Lava Creek	1.50	yes	A	M	4	1992
Frog Rock	3.63	yes	DP	M	6	1992

-Table 4 continued-

PACK	WEIGHT	FLEAS	STATUS	SEX	PACK#	YEAR
Frog Rock	2.08	yes	DP	M	6	1992
Frog Rock	2.08	no	A	M	6	1992
Amethyst	0.86	no	A	M	?	1992*
Druid	3.86	no	A	F	5	1992
Druid	3.40	yes	A	F	5	1992
Oxbow	2.20	no	A	M	2	1992
Oxbow	0.90	no	A	F	2	1992
Oxbow	2.50	no	DKR	F	2	1993
Oxbow	2.50	no	A	M	2	1993
Oxbow	2.27	no	A	F	2	1993
Oxbow	2.27	no	A	M	2	1993
Lava Creek	2.95	no	A	F	2	1993
Deer Creek	2.72	yes	A	F	3	1993
Druid	2.95	no	DCDC	M	5	1993
Druid	2.04	no	DCDC	M	5	1993
Druid	3.40	yes	A	F	5	1993

D?=dead, from unknown cause
DP=Dead, from parvo virus
A= alive
DCDC=Dead, human caused mortality
DCP=Dead, by Chronic peritonitis
DKR=Dead, killed by rancher
* These data were not included in analyses, with the exception of the correlation
    between the number of fleas and the size of the pack; and the number of betas
    per pack correlated with the survival of the pups through August.

Coyote Pack Histories

Eight coyote packs were studied in 1992, and 4 of the eight in 1993 (Table 5).

Norris pack

In 1992 Norris pack consisted of an alpha male (941) who was four years old; an alpha female (840) who was five years old; their daughter, a beta female (070) who was one year old; and a beta male (848) who was eight years old. The pack had eight pups. It is likely that 941 died in January of 1993, because a researcher found his collar which smelled of dead animal. In the spring of 1993, 840 mated with a few males before settling with one. The beta male, 848, was not seen again on the territory after the spring. In 1994, 070, accompanied by an alpha male, took over her mother's territory after 840 was killed by a car. A necropsy done on 840 revealed one fresh placental scar, indicating that she had only one pup in the spring of 1993.

Soda Butte pack

In 1992, Soda Butte pack consisted of an alpha female (958) who was six years old; an unmarked alpha male of unknown age; their daughter a beta female helper (600) who was two years old; a two year old beta male (080) who did not help; a two year old beta female (130) who did not help; and another two year old beta male (140) who did not help. The pack had eight pups in 1992. In 1993, the pack contained the same breeding pair, but the female helper 600 became the alpha

female of a neighboring pack and was replaced in her natal pack by an unmarked beta male. What happened to the betas who did not help is not known. In 1993, their den could not be found.

Druid pack

In 1992, Druid pack consisted of an alpha female (620) who was four years old; an alpha male (860) who was four years old; their pups, a beta male (210) who was one year old; a beta female (280) who was one year old; and an unmarked beta male whose age was unknown. The pack had five pups. In 1993, 860 was killed by a car and the unmarked beta helper became the alpha male. The betas 210 and 280, still were helpers, and an unmarked beta female, who appeared to be a pup from the year before, was a helper. There was also a two year old beta male (240) who did not help, and another unmarked male and female who did not help. In 1993, Druid had five pups.

Oxbow pack

In 1992, Oxbow pack was composed of an alpha female (651), and an alpha male (970) neither of whose age were known. The pack had six pups in 1992. In 1993, 970 was replaced by an unmarked alpha male. It is not clear what happened to 970. Again in 1993 the Oxbow pair had no helpers, and they had five pups.

Table 5. Information on year pack was studied, pack name, pack size, litter size, number of betas per pack, the number of betas who helped per pack, and number of pups that survived through August.

YEAR	PACK	SIZE	LITTER	#HELP	#BETAS	SURVIV
1992	Druid	5	5	3	3	2 8/31
1992	Norris	4	8	2	2	2 8/31
1992	Soda Bte	3	9	1	4	2 8/31
1992	Bison	5	$12	3	4	2 8/31
1992	Oxbow	2	6	0	0	1 7/31
1992	Blacktail	2	4	0	0	2 7/31
1992	Deer Ck	4	6	2	2	0 8/25
1992	Lava Ck	4	7	2	2	1 8/8
**1992	Frog Rk	7	9	5	5	1 8/8
1993	Norris	2	1	0	0	?
1993	Druid	5	5	3	6	2 8/8
1993	Oxbow	2	5	0	0	5 8/8
1993	Deer Ck	3	4	1	1	4 8/8
1993	Lava Ck	2	5	0	0	5 8/8

* pack size includes only alpha pair and beta helpers
$ a double litter from the alpha female and her daughter,298
** Frog Rock pack's data were not calculated in analyses,
  with the exception that the number of betas was compared with the survival
  of the pups, and the initial litter size was compared with the number of
  betas per pack.

Bison pack

In 1992, Bison pack consisted of an alpha female (570) who was ten years old; an alpha male (740) who was four years old; 570's daughter (298) who was two years old; an unmarked beta female who appeared to be a pup from the year before; a beta male (060) who was one year old; and an unmarked beta male of unknown age who did not help. The pack had a double litter from 570 and 298 of twelve pups, though 570 was still considered the alpha female. In 1993, the den was not found, but two pups were seen at the end of the season. The pack then was made up of an beta male of unknown age; a two year old beta male; a one year old beta of unknown sex; a one year old male and female; the same unmarked beta female helper; 298; 570; 740; and 060. The three one-year-olds appeared to be pups from the year before.

Deer Creek pack

Deer Creek pack was composed of an alpha female, an unmarked alpha male, a beta male (560), and an unmarked male in 1992, none of whose age were known. The pack had six pups. In 1993, there were the same alpha male and female, but they had 560 only as a helper and they had four pups. It is unknown what happened to the unmarked beta helper.

Blacktail pack

In 1992, Blacktail pack consisted of only an alpha male (510), and an unmarked alpha female, both of unknown age. The pack had four pups. In 1993, both the male and female were replaced by coyotes from a neighboring pack. The signal from 510 was picked up out of the Park. The alpha female's whereabouts was unknown. Though the den was not found in 1993, another Park researcher saw four pups (S. Houser, personal communication).

Lava Creek

The Lava Creek pack was composed of an unmarked alpha female and alpha male; and an unmarked beta male and female helper, all of unknown ages. In 1992 the pack had seven pups. In 1993, the same breeding pair had no helpers and had five pups. What happened to the two helpers from 1992 is not known.

Adult Roles

All adults who helped to rear the young were seen playing with, socializing with, feeding, and guarding the pups (Table 6). There was only one case where a beta helper was seen grooming the young, usually this was done by either the alpha male or the alpha female. Defending the territory was done mostly by the alpha male,

but the alpha pair and the beta helpers would defend the pups from potential predators (Appendix). All adults that helped showed signs of being alert while in the den area. There were two instances where a beta or the alpha male was seen regurgitating to the alpha female while she was lactating and rarely left the den. All adults who helped were seen entering the den, but only after the pups were being nursed outside of the den. During the first period, when the pups were nursed inside the den, only the alpha female was seen entering. There were betas who did not help to rear the pups, and they were rarely, if ever, seen in the den area, but they were seen elsewhere on the territories.

Table 6. Mean hourly rates of alpha females and alpha males, beta females and beta males spent playing with, socializing with and feeding the pups for the summer; and the percent of time each spent guarding the pups and being alone with them.

SocialClass	Play	Socialize	Regurgitate	B Food	Guard	Alone
*Afemale	1.32	0.83	0.16	0.23	0.49	0.37
Amale	1.66	0.86	0.31	0.15	0.46	0.30
Bfemale	0.63	0.17	0.03	0.47	0.28	0.11
Bmale	0.24	0.38	0.07	0.42	0.19	0.07

*Afemale=Alpha female
Amale=Alpha male
Bfemale=Beta female
Bmale=Beta male
B food=Bring whole prey

Background of helpers

The non-breeding beta helpers were either one or two years old, however there was one case where the beta was eight. Out of fourteen betas, seven (50%) were females. Ninety percent of coyote females that are over 20 months old become sexually active (Gier 1975). Although they are physiologically capable of mating at ten months, the first successful breeding in unexploited populations usually occurs between 2-4 years old (Crabtree 1989). There was only one case in which both a beta and an alpha female had pups in the same pack. The betas may leave the pack for a few months during the winter, then come back to help the following year. Out of fourteen helpers, at least 86% (12) were known positively to be the pups from a previous litter of an alpha pair they had helped.

Differences between alpha males, alpha females, and betas: Hypothesis 1

Hypothesis 1 stated: Most betas and all alphas help to rear pups. There will be a difference in behaviors among the different levels of social class and the different sexes.

Alpha females compared with alpha males

There were few statistically significant differences when comparing all alpha females with all alpha males. Alpha females spent significantly more time alone at the den during period one (t-test, t=1.8, df=9, P =0.09) (Figure 3) than did alpha males. Also, the alpha females spent more time howling during period three than did the alpha males (Wilcoxon, P =0.04), and more time playing with the pups (Wilcoxon, P=0.07) (Table 7).

Table 7. The P-values and the means of behaviors analyzed when comparing alpha females with alpha males for each period.

	Prsnt	Alne	Alert	Howl	Grm	Play	Socl	Regr	B Fd
1									
P=	0.32	**0.09**	0.50	0.45	0.46	0.46	0.46	0.36	0.99
AF=	0.35	**0.28**	0.09	0.10	0.008	0.03	0.03	0	0
AM=	0.23	**0.12**	0.16	0.03	0	0	0	0.46	0
2									
P=	0.17	0.32	0.46	0.57	0.88	0.59	0.20	0.58	0.91
AF=	0.22	0.12	0.13	0.52	0.11	0.29	0.09	0.27	0.11
AM=	0.29	0.17	0.16	0.46	0.25	1.18	0.31	0.18	0.07
3									
P=	0.27	0.29	0.62	**0.04**	0.18	**0.07**	0.94	0.56	0.99
AF=	0.22	0.18	0.31	**0.59**	0.15	**1.46**	1.00	0.02	0.19
AM=	0.17	0.14	0.36	**0.02**	0.19	**1.40**	1.00	0.33	0.19

P= P-values
AF=The alpha females (means of)
AM=The alpha males (means of)
Alne=Alone
Grm=Groom

Socl=Socialize
Regr=Regurgitations
B Fd=Bring whole food

Alpha females with betas compared with alpha males with betas

Tests run on alpha females in packs with betas, compared with alpha males in packs with betas showed that females spent more time at the den during period one than did males (t-test, t=2.13, df=5, P=0.08) (Table 8), and that females were alone more at the den during period one (t-test, t=3.55, df=5, P =0.01) than were males.
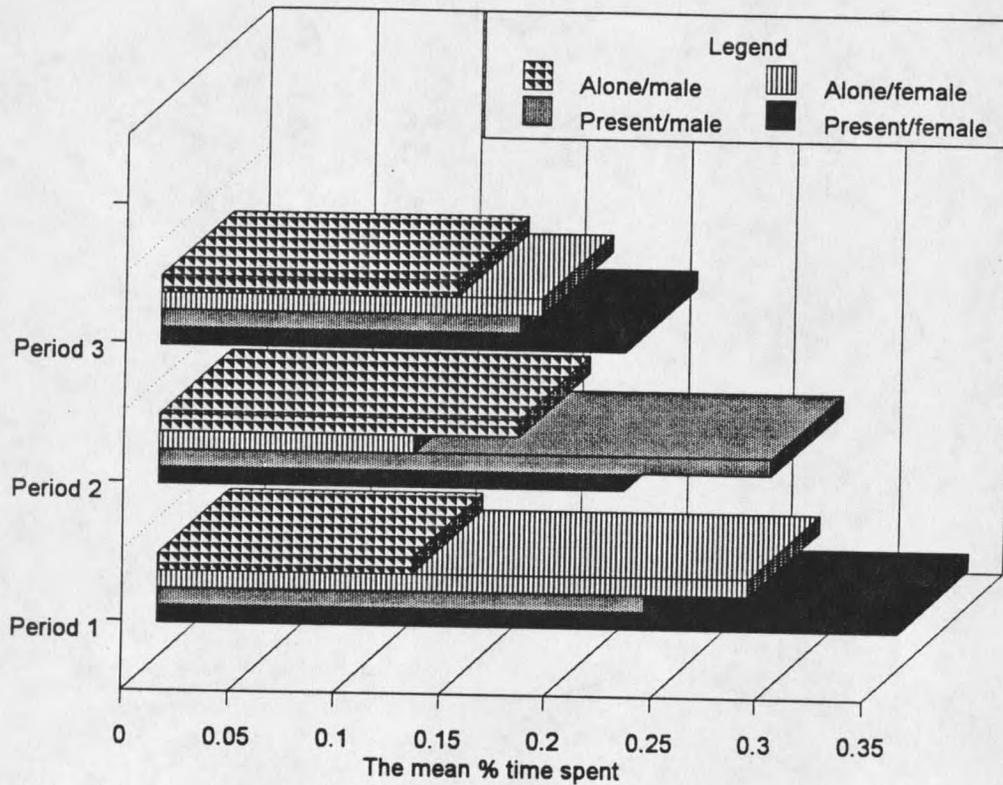
Figure 3. The mean percent of time the alpha female and alpha male spent present, and alone at the den during periods one, two,and three.

Table 8. The P-values and the means of the behaviors analyzed when comparing alpha females with betas, with alpha males with betas.

Perid	Prsnt	Alne	Alert	Howl	Grm	Play	Socl	Regr	B Fd.
1									
P=	**0.08**	**0.01**	0.71	0.84	0.99	0.56	0.56	0.99	0.99
AF=	**0.37**	**0.27**	0.13	0.13	0	0.04	0.05	0	0
AM=	**0.17**	**0.07**	0.09	0.05	0	0	0	0	0
2									
P=	0.54	0.57	0.68	0.30	0.81	0.89	0.38	0.13	0.99
AF=	0.25	0.15	0.13	0.64	0.03	0.38	0.11	0.44	0.12
AM=	0.29	0.19	0.16	0.35	0.32	1.51	0.29	0.19	0.09
3									
P=	0.99	0.78	0.93	0.24	0.38	0.43	0.85	0.56	0.12
AF=	0.17	0.11	0.32	0.38	0.10	1.52	2.33	0	0.26
AM=	0.17	0.12	0.34	0.04	0	0.15	1.90	0.60	0

Perid=Period
Prsnt=Present
Alne=Alone
Grm=Groom
Socl=Socialize
Regr=Regurgitation
B Fd.=Bring whole food
P=P-values
AF=Alpha females with betas (means of)
AM=Alpha males with betas (means of)

Alpha females without betas compared with alpha males without betas

There were no significant differences between alpha females without betas and alpha males without betas (Table 9) .

Table 9. The means and P-values in the differences in behavior between alpha females without betas, with alpha males without betas.

Period	Present	Alone	Alert	Howl	Groom	Play	Socialize	Regurg.	B.Fd.
1				(					
P=	0.94	0.73	0.40	0.99	0.99	0.99	0.99	0.99	0.99
AF=	0.30	0.30	0.02	0	0	0	0	0	0
AM=	0.33	0.20	0.26	0	0	0	0	0	0
2									
P=	0.41	0.22	0.11	0.24	0.88	0.35	0.18	0.61	0.61
AF=	0.16	0.09	0.11	0.41	0.23	0.20	0	0.04	0.11
AM=	0.24	0.17	0.19	1.20	0.17	0.59	0.35	0.07	0.17
3									
P=	0.23	0.40	0.77	0.12	0.75	0.78	0.43	0.43	0.93
AF=	0.22	0.20	0.34	1.00	0.22	1.78	0	0	0.19
AM=	0.17	0.16	0.38	0	0.38	2.73	0.03	0.06	0.18

Alpha males with betas compared with alpha males without betas

The only statistical difference between alpha males with betas compared with alpha males without betas, was that males without betas howled more during period two (Wilcoxon test, P =0.07) than did those with betas (Table 10).

Table 10. The P-values and the means of behaviors analyzed when comparing alpha males with betas, with alpha males without betas.

Per	Prsnt	Alne	Alert	Howl	Grm	Play	Socl	Regr	B Fd.
1									
P=	0.53	0.47	0.42	0.68	0.99	0.99	0.99	0.99	0.99
AW=	0.17	0.07	0.09	0.05	0	0	0	0	0
AO=	0.33	0.20	0.26	0.	0	0	0	0	0
2									
P=	0.53	0.81	0.70	**0.07**	0.53	0.92	0.92	0.75	0.91
AW=	0.29	0.19	0.16	**0.35**	0.32	1.50	0.29	0.19	0.09
AO=	0.24	0.17	0.19	**1.20**	0.17	0.59	0.35	0.07	0.17
3									
P=	0.90	0.38	0.75	0.45	0.45	0.99	0.40	0.99	0.18
AW=	0.17	0.12	0.34	0.04	0	0.15	1.90	0.60	0
AO=	0.17	0.16	0.38	0	0.38	2.73	0.03	0.06	0.18

Per=Period
Prsnt=Present
Alne=Alone　　　　　　　　　　P=P-value
Grm=Groom　　　　　　　　　　AW=Alpha males with betas (means of)
Regr=Regurgitation　　　　　　AO=Alpha males without betas (means of)
B Fd.=Bring whole food
Socl=Socialize

Alpha females with betas compared with alpha females without betas

For alpha females with betas compared with alpha females without betas, females with betas socialized more with the pups than did those females without betas during period two (Wilcoxon test, P =0.10) and during period three (Wilcoxon, P=0.06), and they regurgitated more (Wilcoxon test, P =0.03) during period two. Females without betas were alone at the den more (t-test,t=-2.68, df=4, P =0.05)

than were females with betas in period three (Table 11).

Table 11. The P-values and means of behaviors analyzed when comparing alpha
females with betas, with alpha females without betas.

Per.	Prsnt	Alne	Alert	Howl	Grm	Play	Sclz	Regr	B Fd.
1									
P=	0.60	0.80	0.41	0.41	0.99	0.72	0.72	0.99	0.99
AW=	0.37	0.27	0.13	0.13	0	0.04	0.05	0	0
AO=	0.30	0.30	0.02	0	0	0	0	0	0
2									
P=	0.17	0.39	0.70	0.70	0.32	0.53	**0.10**	**0.03**	0.74
AW=	0.25	0.15	0.13	0.64	0.03	0.37	**0.11**	**0.43**	0.12
AO=	0.16	0.09	0.11	0.41	0.23	0.20	**0**	**0.04**	0.11
3									
P=	0.47	**0.05**	0.92	0.82	0.64	0.66	**0.06**	0.99	0.99
AW=	0.17	**0.11**	0.32	0.38	0.10	1.52	**2.32**	0	0.26
AO=	0.22	**0.20**	0.34	1.00	0.22	1.78	**0**	0	0.19

Per.=Period
Prsnt=Present
Alne=Alone
Grm=Groom
Sclz=Socialize

Regr.=Regurgitation
B Fd.=Bring whole food
P=P-value
AW=Alpha females with betas
AO=Alpha females without betas

Beta females compared with beta males

   A Students t-test showed that beta females spent significantly more time at the den during period one (t=2.6, df= 7.0, P =0.03), than did beta males. Beta females, during period three, spent significantly more time alone at the den (t=2.0, df=8.0, P =0.07) than did beta males, and beta males were more alert at the den (t=-2.07, df=8.0, P =0.07) than were beta females (Table 12) (Figure 4).

Table 12. The P-values and the means of behaviors analyzed when comparing beta females with beta males.

Per	Presn	Alone	Alert	Howl	Play	Soclz	Regur	B Fd
1								
P=	**0.03**	0.92	0.45	0	0.40	0.43	0	0
BF=	**0.49**	0.07	0.14	0	0	0.05	0	0
BM=	**0.22**	0.07	0.28	0	0.17	0.84	0	0
2								
P=	0.93	0.52	0.67	0.34	0.24	0.54	0.63	0.28
BF=	0.24	0.16	0.20	0.03	0.90	0.34	0.10	1.26
BM=	0.25	0.12	0.17	0.17	0.26	0.19	0.16	0.14
3								
P=	0.78	**0.07**	**0.07**	0.44	0.27	0.98	0.44	0.47
BF=	0.12	**0.09**	**0.16**	0	1.00	0.11	0	0.14
BM=	0.10	**0.02**	**0.40**	0.17	0.30	0.12	0.05	1.11

Per.=Period
P=P-values
BF=Beta female (means of)
BM=Beta males (means of)
Presn=present
Soclz=Socialize
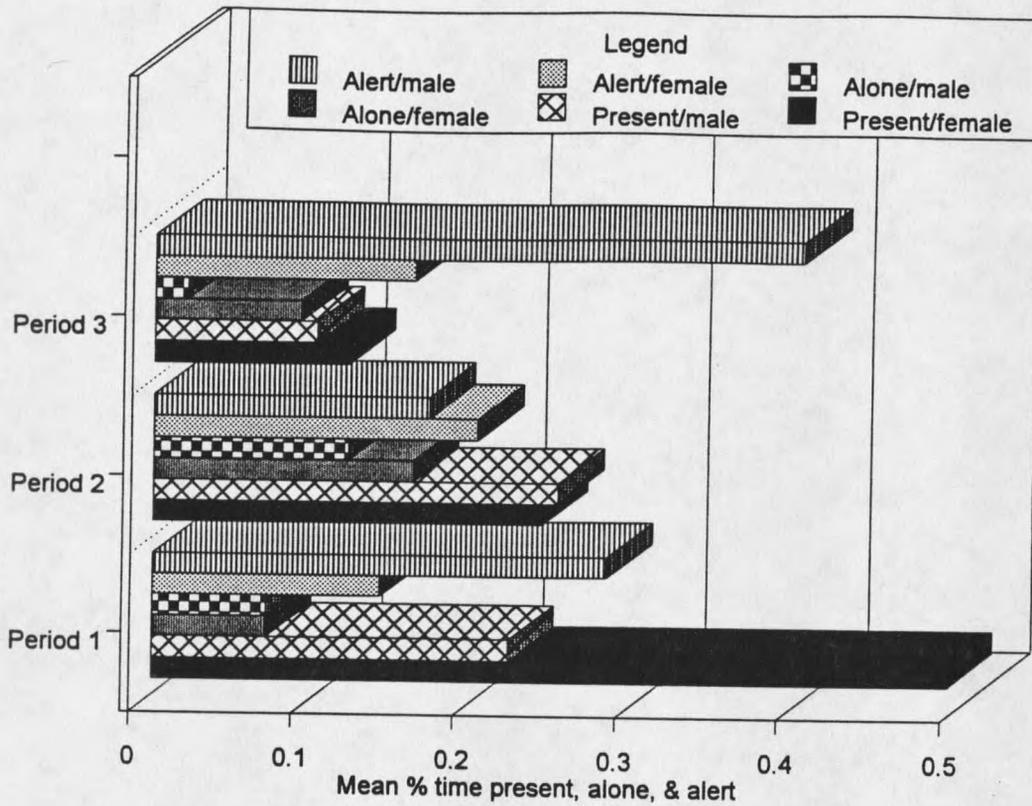Regurg=regurgitate
B Fd= Bring whole prey

Figure 4. The mean percent of time female betas compared with male betas spent present, alone, and alert at the den during periods one, two, and three.

Differences between packs with different numbers of betas

When the coyote packs were divided into those with 0, 1, 2, and 3 betas, the size of the samples were too small to test statistically. Therefore, graphs (Figure 5-7) and tables (Table 13 & 14) were made for the mean percentage of time present, alone and alert at the den during each period, and the amount of time pups were guarded.

Table 13. Mean percentage of time coyotes were present at the den; alone at the den; and alert at the den. Divided into packs with no betas, one beta, two betas, and three betas.

PERID	O BETAS			1 BETA			2 BETAS			3 BETAS		
ONE	P	A	T	P	A	T	P	A	T	P	A	T
*AF	0.30	0.20	0.02	-	-	-	0.30	0.30	0.11	0.45	0.33	0.18
AM	0.33	0.20	0.09	-	-	-	0.23	0.10	0.03	0.03	0.03	0.01
B	0	0	0	-	-	-	0.24	0.07	0.06	0.42	0.09	0.04
	(N=2)			(N-0)			(N=2)			(N=2)		
TWO												
AF	0.16	0.08	0.02	0.21	0.19	0.08	0.22	0.11	0.04	0.30	0.20	0.09
AM	0.28	0.14	0.04	0.19	0.15	0.03	0.27	0.08	0.02	0.44	0.40	0.31
B	0	0	0	0.14	0.09	0.04	0.31	0.14	0.04	0.20	0.10	0.02
	(N=4)			(N=2)			(N=3)			(N=3)		
THREE												
AF	0.22	0.19	0.08	0.13	0.11	0.04	-	-		0.24	0.18	0.09
AM	0.17	0.16	0.06	0.18	0.14	0.08	-			0.17	0.10	0.06
B	0	0	0	0.03	0.03	0.01	-	-		0.17	0.07	0.06
	(N=3)			(N=1)			-			(N=3)		
							-	-				
							-					
							(N=0)					

* P= Mean percentage of time present at the den **AF= Alpha female
A= Mean percentage of time alone at the den   AM= Alpha male
T= Mean percentage of time alert at the den   B=Betas combined
PERID=Period

Table 14. Mean percentage of time the pups are guarded; the mean hourly rate pups are regurgitated to; and the mean hourly rate the pups are brought hard food, by all members of the pack combined. Divided into packs with 0, 1, 2, and 3 betas.

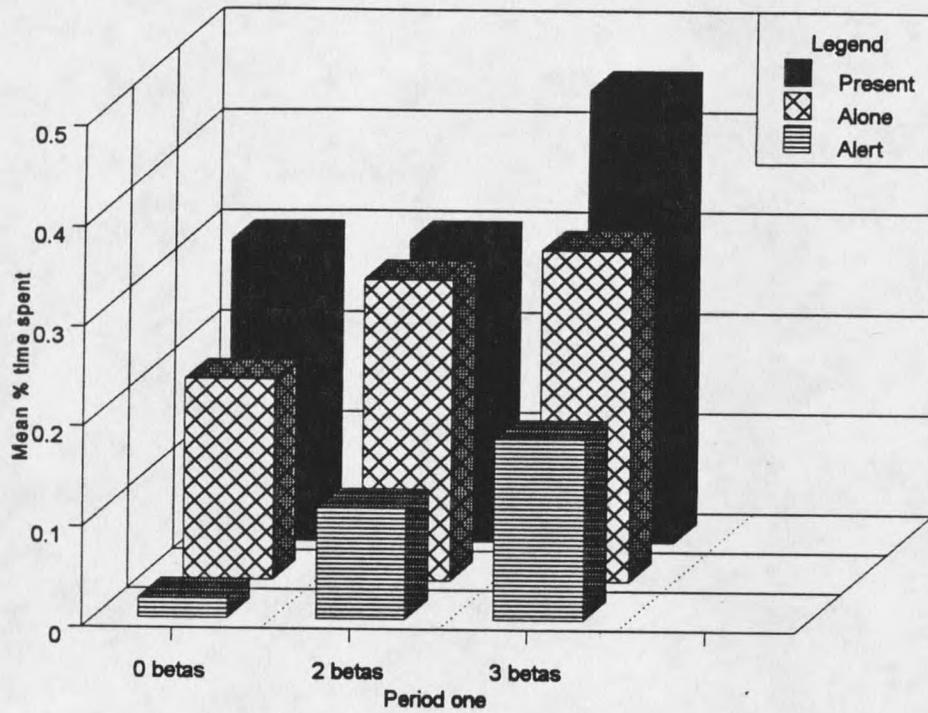| PERIOD	0 BETAS			1 BETA			2 BETAS			3 BETAS		
	*G	R	D	G	R	D	G	R	D	G	R	D
ONE	0.63	0	0	-	-	-	0.77	0	0	0.90	0	0
TWO	0.44	0.19	0.18	0.54	0.87	0.29	0.80	0.85	3.8	0.94	0.27	0.30
THREE	0.39	0.27	0.39	0.34	0.57	0.34	-	-	-	0.58	0.19	0.47

*G= Guard
R= Regurgitate
D= Bring hard food

Figure 5. The mean percent of time present, alone, and alert at the den during period one for alpha females in packs with no, two, and three betas.
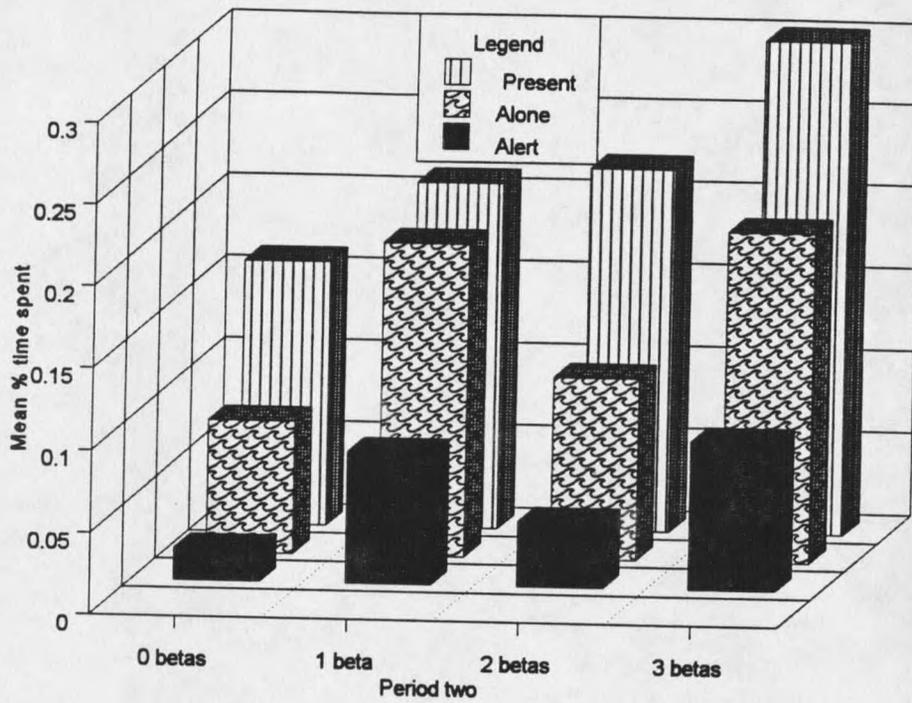
Figure 6. The mean percent of time present, alone, and alert at the den in packs for alpha females during period two in packs with no, one, two, and three betas.
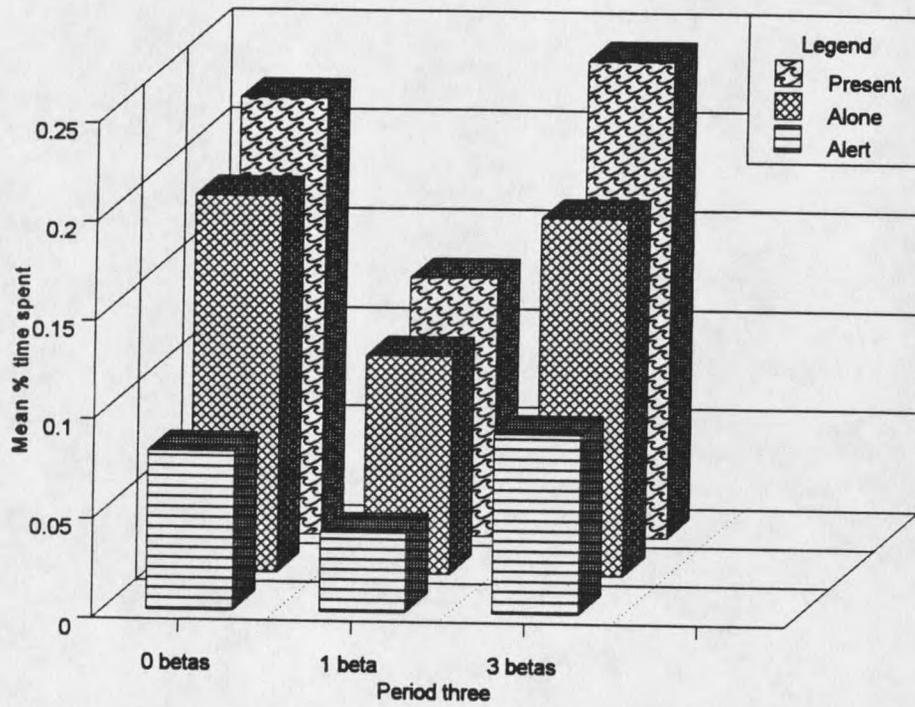
Figure 7. The mean percent of time present, alone, and alert at the den for alpha females in packs with no, one, and three betas, during period three.

Comparisons of rates of provisionings to the pups

Alpha females of a pack provisioned significantly more to the pups (Kruskal-Wallis, x^2=6.3, df=1, P =0.01) than did the betas. Alpha females also provisioned more than did the alpha males of a pack (Kruskal-Wallis, x^2=6.5, df=1, P =0.01). The alpha pair in packs with betas provisioned significantly more to the pups than did the betas of the pack (Kruskal-Wallis, x^2=2.7, df=1, P =0.09) (Table 15.). There was no difference between the rates of feedings from alpha females compared with alpha males (Kruskal-Wallis, x^2=.866, df=1, P=0.35), or between the rates of feedings from the betas and the alpha females (Kruskal-Wallis, x^2=.006, df=1, P=0.98).

Table 15. Comparisons of rates of feedings from different pack members.

	Alpha females	Alpha males	Betas	Alpha Pair
Alpha females	N/A	P=0.35	P=0.98	N/A
Alpha males	*P=0.01	N/A	P=0.57	N/A
Betas	*P=0.01	P=0.57	N/A	P=0.09
Alpha Pair	N/A	N/A	P=0.09	N/A

P=P-values
*=Nursings from alpha females have been added

Phenology of Denning Behavior: Hypothesis 2

Hypothesis 2 stated: The proportion of time the alphas and the betas are present at the den, and alone with the pups will change as the pups grow. There were no significant differences in the amount of time present at the den for the alpha females

across time (Kruskal-Wallis, x^2=3.71, df=2, P =0.15), or for the alpha males across time (Kruskal-Wallis test, x^2=3.68, df=2, P =0.15). There were significant differences in the amount of time beta females (Kruskal-Wallis test x^2=8.07, df=2, P =0.01), and beta males (Kruskal-Wallis test x^2=4.64, df=2, P =0.09) spent present at the den between periods. For the percentage of time a coyote of a social class was alone at the den, there was a significant difference between periods for the alpha females (Kruskal-Wallis test, x^2=6.34, df=2, P =0.04,), for the beta females (Kruskal-Wallis test, x^2=0.42, df=2, P =0.01), and for the beta males (Kruskal-Wallis, x^2=6.0, df=2, P =0.04), but was not for the alpha males (Kruskal-Wallis test, x^2= 1.38, df=2, P =0.50). Alpha females with betas showed a significant difference in the amount of time present from period to period (Kruskal-Wallis,x^2 =4.57, df=2,P=0.10) , but there was not for alpha males with betas, for alpha males without betas, or for alpha females without betas. There was no significant difference between periods one and two only for alpha males and females with or without betas.

Age of betas and Number of Pups: Hypothesis 3

Hypothesis 3 stated: The age of the betas and the size of the litter will affect the amount of time the betas spend with the pups. There was no significant correlation (Spearman r= 0.18, N=17, P =0.63) between the age of the betas and the amount of time they spent helping. Nor was there a significant correlation between the

number of young in the litter compared with the mean percentage of time the betas helped over the summer (Spearman r = 0.29, N=17, P =0.25), or between the age of the betas compared with the number of regurgitations and bringing of food they did over the summer (Spearman, r=0.-23, P =0.49).

Benefits to the Alpha Pair from having Helpers:Hypothesis 4

Hypotheses 4 stated: The alpha pair will benefit from the presence of betas. The rates of regurgitations and the bringing of food were combined. The analyses were not broken into periods because results for overall contributions were wanted. The correlation between the size of the pack compared with the initial litter size was significant (Spearman r=0.55, N=14, P =0.04). There was a significant positive correlation between the number of feedings from the alpha pair and the betas and the size of the litter (Spearman r= 0.72, N=12, P =0.007). For the percent of time alpha males and females were present at the den compared with the number of betas per pack, there was a non-significant positive correlation (Spearman r =0.45, N=12, P =0.13) (Figure 8). There was a non-significant negative correlation between the rates of nursings of the alpha females and the number of betas per pack (Spearman r = -0.50, N=12, P =0.11) (Figure 9). There was a positive correlation between the number of feedings from the alpha female of a pack and the number of pups in a litter (Spearman r=0.58, N=12, P=0.04). There was a non-significant negative correlation for the rate of regurgitations by the alpha male in relation to the number of betas in the pack (Spearman r=-0.43, N=12, P =0.15).
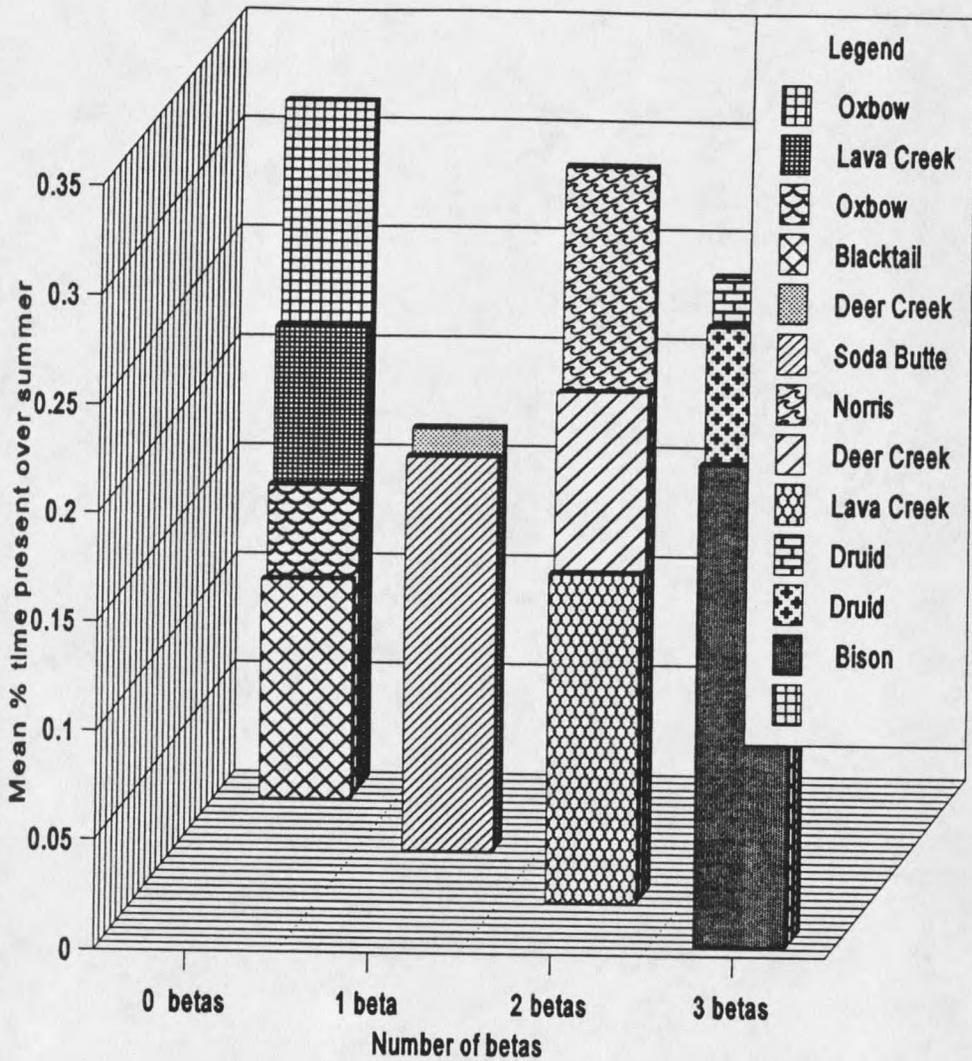
Figure 8. The mean percentage of time at the den over the summer for alpha males plus alpha females compared with the number of betas per pack.
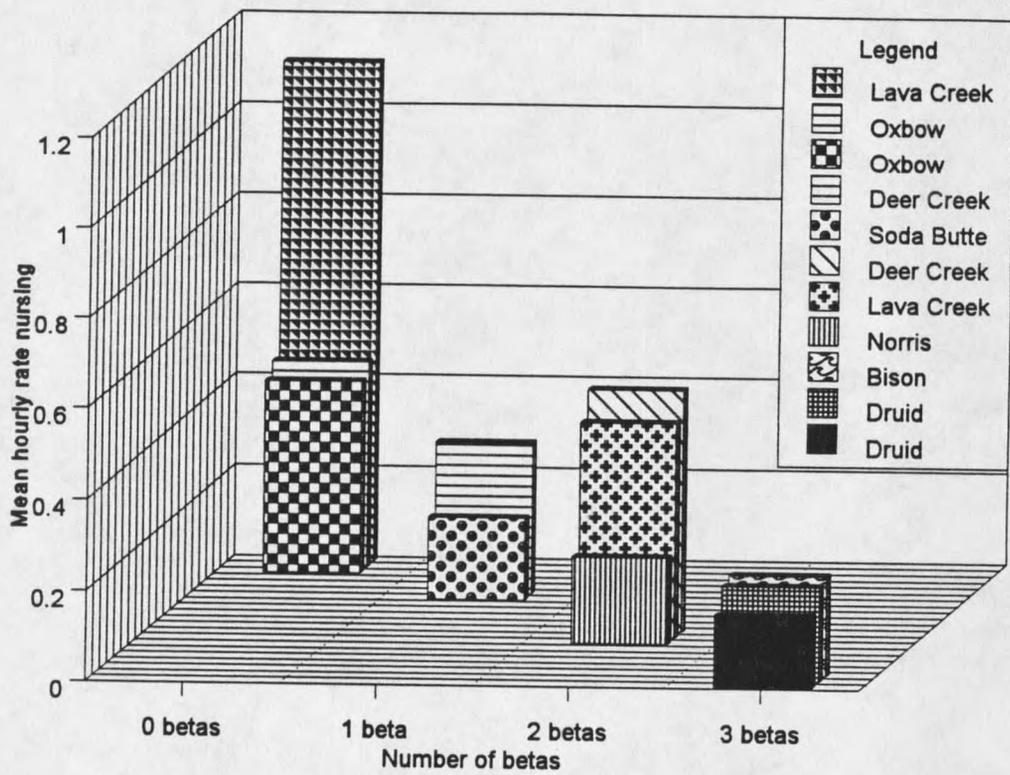
Figure 9. The mean hourly rates of nursings over the summer by the alpha females compared with the number of betas per pack.

Survival of the Pups:Hypothesis 5

Hypothesis 5 stated: The presence of betas will benefit the current pups, by an increase in their rate of survival, their rate of food intake, and by a decrease in the amount of time they are left alone. There was a negative correlation between the number of betas in a pack and the survival of the pups until August (Spearman r= -0.51, N=15, P =0.07), however, in 1992 the pups suffered high mortality associated with an outbreak of Parvo virus. This seemed to affect packs regardless of size, and may have obscured a significant relationship. There was a weak positive correlation between pack size and the presence of fleas found on puppies (Spearman r=0.20, N=60, P =0.16). For alpha females, alpha males, and betas combined there was a significant correlation (Spearman r = 0.59, N=12, P =0.04) between the number of betas per pack, and the rates of feedings to the pups (Figure 10). There was a significant difference in the percent of time the pups were left alone and the size of the pack (Spearman r = -0.66, N=12, P =0.01) (Figure 11). There was no correlation between the size of the pack and the weight of the pups at capture (Spearman r=0.06, N=50, P =0.66).
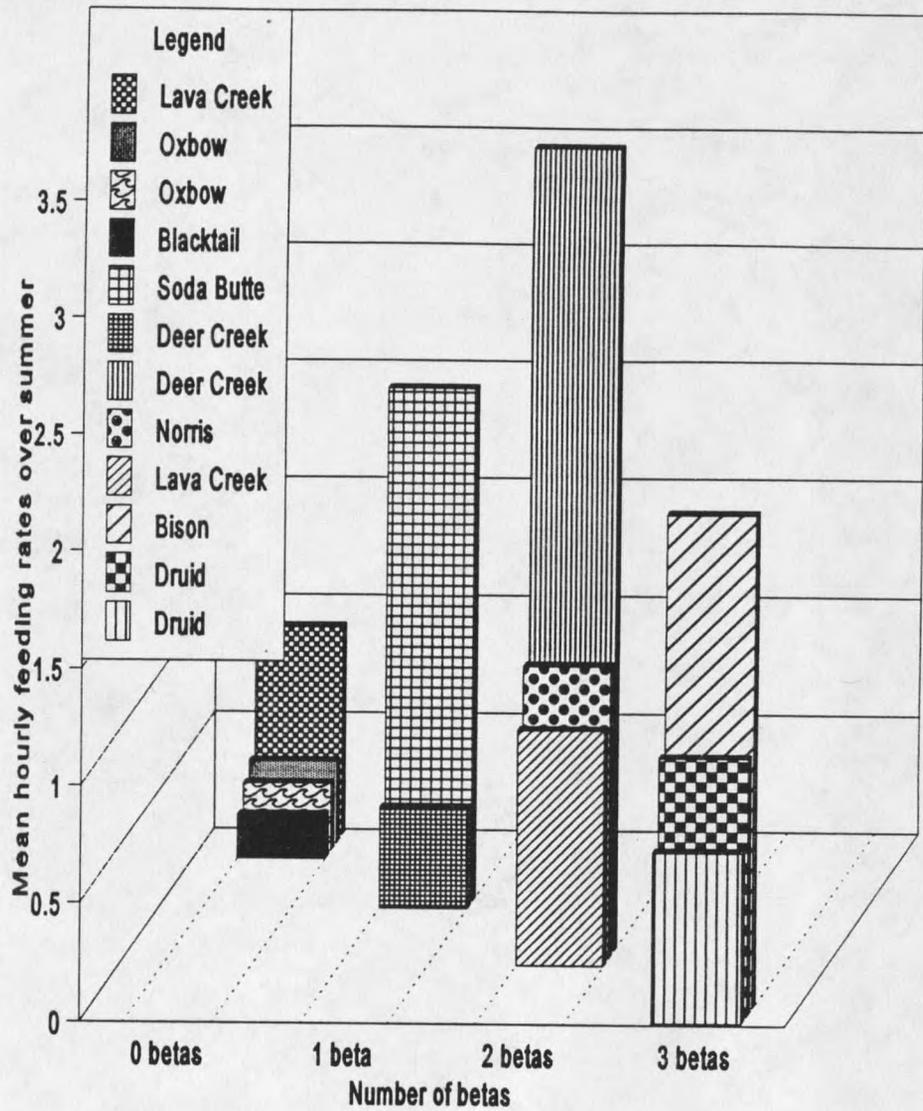
Figure 10. The mean hourly rates of feedings for the pups over the summer compared with the number of betas per pack. This adds the feedings by the alpha male, the alpha female, and the betas of a pack together.
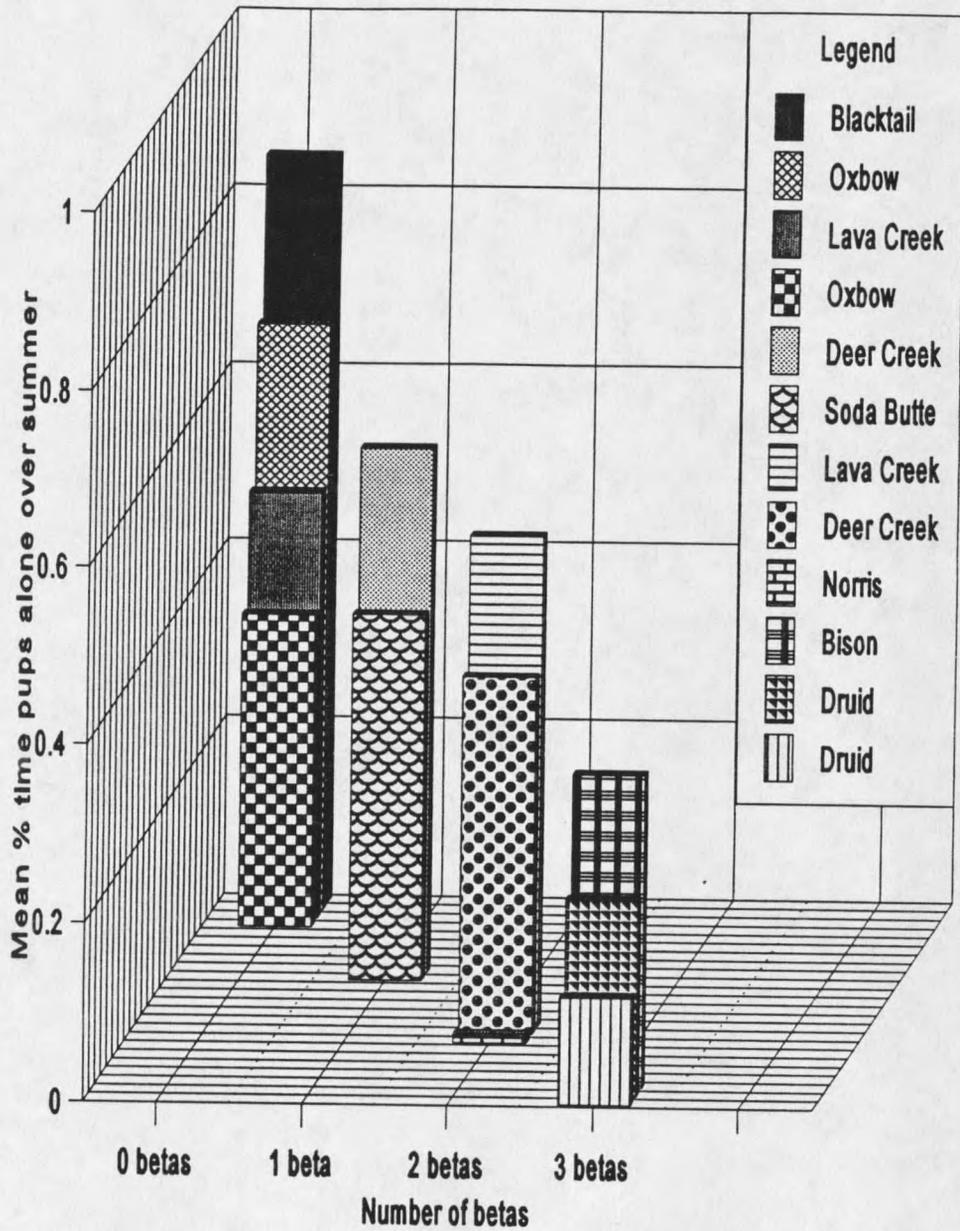
Figure 11. The mean percentage of time pups are alone over the denning season, compared with the number of betas.

DISCUSSION

The process of helping at dens in coyote packs can be understood better by looking at the contributions of the helpers to the breeders, the contributions of the helpers to the young, and the contributions of helping to the helpers themselves. These contributions are not mutually exclusive, but rather they build on top of one another for an overall benefit to the pack.

Differences between alpha females and alpha males: Hypothesis 1

Much of the results to hypothesis 1 tie into the results of hypothesis 4 directly. Therefore, most of hypothesis 1 will be discussed under the category of hypothesis 4.

During period one alpha females spent significantly more time alone at the den than did alpha males, because females alone nurse the pups. The pups form of nourishment, during the first period, comes mostly from their mothers milk. They spend the majority of their time in the den, therefore, the presence of the alpha male does not contribute directly to their survival. The means of the second period showed a decrease in the amount of time alpha females spent at the den, and an increase in the amount of time alpha males spent at the den. Jurke and Pryce (1994) found in Goeldi's monkeys (*Callimico goeldii*) that there is an increasing independence of the young from the mother 6 weeks or more after birth. In these monkeys, the time the young spent on the father's back increased in parallel with the

decrease in time spent on the mother's back, beginning in week three and reaching a maximum in week five. Moehlman (1985) found with jackals (*Canis mesomelas, C. aureus*) the amount of time the mother spent at the den decreased, and the amount of time the male spent at the den increased after the pups were three weeks old. The decrease in the amount of time the alpha female spent at the den during period two, from period one, may allow her more time to feed and to rest to make up for the energetic drain of pregnancy and lactation. Whereas the male, during period one, may be resting or defending the territory, thus preparing himself for the responsibility of caring for the pups during period two. These strategies of the alpha pair indicate a division of labor. During period three, the pups rarely used their den. They used, rather, a postdenning-rendezvous site, similar to those used by wolf pups (*Canis lupus*) (Mech, 1970). The alpha male and alpha female spent the least time, of the three periods, about the den at this point. However, the means show they were the most alert during this period. Coyote pups were quite curious and active during the third period, so they may have been more obvious to predators. Nonetheless, they were fairly alert and could run fast. This enabled them increasingly to rely on themselves for protection and to rely less on their parents. A sharpening of the pups' senses may account for the decrease in the amount of time the alpha pair spent about the den. (Mech 1970) writes that wolf adults often were away during the pups postdenning rendezvous-site period. Alpha females howled significantly more than did alpha males during period three (but did not during the other two periods). This may have served to keep pups within a certain area. The mean rate of howling for alpha females was greatest

during period three. For the males it was greatest during period two. The lowest mean rate of howling, for both adults, was during period one. The adults may howl the least during this first period in order to keep the location of their den-bound pups unknown to predators. Furthermore, the mean rate of howling, over the summer, for alpha pairs without betas (.44) was greater than the mean rate of howling for alpha pairs with betas (.27). A higher rate of howling, by alpha pairs without betas, may help to deter predation on the pups, if the howling serves to alert predators that the alpha pair are guarding. The presence of betas may alleviate the need of the alpha pair to advertise their occupancy of the territory and their guarding of their pups. There was only one pup that was known to have been killed by a predator.

Phenology of Denning Behavior:Hypothesis 2

Early winters in Yellowstone Park force most animals to be competent at surviving soon on their own. The three periods of the summer, necessarily are ones of rapid growth for the pups. This supports what Mech (1970) discovered in wolf pups; that is, the first fourteen weeks are the period of maximum growth. This quick development requires the adults to change their behaviors according to the changing needs of their pups. There was a significant difference in the amount of time alpha females with betas spent present from period to period. There was also a significant difference between the amount of time the female alphas and the female and male betas were alone from period to period. Alpha females, usually, are the only coyotes in the pack that nurse. Therefore, beta females, during period

one, may have used this time of neonatal care to learn "motherhood." During period two, when alpha males and beta males spent more time with the pups than they did in period one, the beta females and alpha females with betas were able to spend significantly less time. It is during period two that the adults started to wean the pups, to play with them, to howl more and to bring them regurgitated and later solid food. The pups, during the second period, may have needed more guarding because they were active and out of the den, yet not very alert. Mech (1970) writes that wolf pups can control their body temperatures much better at this age (about 4-6 weeks) than they can during the neonatal period, which enables them to spend time outside.

During period three the betas presence was not so important. The pups had started to pounce on their own, some of the first signs of learning to hunt, and were fairly alert, so the percentage of time the adults spent present at the den dropped. Andelt et al. (1979) wrote that in Illinois coyotes the 1-15th of July constitute the period of pup training. During period three, when the pups spent little time in their den, the betas spent the least amount of time in the den area. Therefore, they were not involved in much of the pups training at this point. Harrison and Gilbert (1985) found that in July, after the pups had abandoned their dens, yet still remained at a rendezvous-site, the adults returned initially to rendezvous sites one or two times daily, but then visits became progressively less frequent as pups developed.

Age of the Betas and the Number of Pups:Hypothesis 3

There was no correlation between the age of betas and the amount of time the betas spent at the den, between the number of pups in the litter and the amount of time the betas spent at the den, or between the number of regurgitations and bringing of food and the age of the betas. Most of the betas were one or two years old, which is an indication that once they reach a certain age they disperse. The first two years of their lives appear to be important years for learning, so not much difference in helping behaviors from year one to year two would be expected.

Benefits to the Alpha Pair:Hypothesis 4

There was no correlation between the number of provisionings from the alpha female and the size of the pack. Therefore, the size of the pack did not decrease the amount of time that the female spent feeding the pups. In Moehlman's work with jackals (1985) she found that there was no change in the number of alpha regurgitations, or in the bringing of food to the pups in packs with helpers, but she found that the alpha female got more regurgitations while she was pregnant in packs with helpers. There was a non-significant negative correlation $(r=-.50, P=0.11)$ between the number of betas per pack and the amount of time an alpha female spent nursing.

Altmann (1983), in her study on the costs of reproduction for baboons (*Papio cyncephalus*), wrote;

> "It is known that women who lactate successfully and whose
> caloric intake during lactation is 23% over their normal
> maintenance intake do not maintain their body weight,
> whereas at 32% over normal intake, lactating women maintain
> steady body weight. If such weight losses occur in baboons,
> insufficient nutrition and weight loss may be a major source of
> maternal susceptibility to death and may place severe limits
> on the length and intensity of the lactational period
> unless females are able to store an appreciable supply of
> excess fat during pregnancy."

It is likely that coyotes have similar reproductive problems as baboons and other mammals. Alpha females without betas may have faced greater physiological stresses during gestation and after pregnancy. They may have had an increased need to forage in order to keep up their weight and the length of the lactational period, and they had no betas to regurgitate to them when they were unable to leave the den frequently. The first snows may come into Yellowstone Park as early as August, and the ground squirrels, a prime source of food during the denning season, then begin to hibernate. Those females whose body weight was low, or who had a physically stressful summer lost an easy source of food with the hibernation of the ground squirrels. If females had a physiologically stressful summer, they may have a harder winter and consequently a shorter life span. Konig (1994) found that females body weight in the house mouse (*Mus musculus*) is important for future reproduction, and that heavier females at weaning tend to have larger litters. Moehlman (1983) found that female jackals may also improve their own future reproductive success by tolerating helpers because helpers may alleviate their

nutritive stress through the lactation period. Millar (1977) wrote that one way mammals that are limited in energy during reproduction could handle further energy restrictions is by reducing the size of their litter. Because coyotes in smaller packs had significantly smaller litters there may be a positive correlation between the amount of energy a female has to use during reproduction and the size of her pack. The positive correlation between the size of the pack and the initial litter size may also have been related to the health of the alpha female when she conceived, and to the presence of betas to help with feeding and guarding the young. Martin (1984), wrote that parental investment should be measured as the rate of milk-transfer, or daily suckling bouts, and that weaning should be considered to be the phase of parental care during which the rate of parental investment drops most sharply. Furthermore, with Goeldi's monkeys (Jurke & Pryce 1994), females that feed less will transfer the infant earlier to the care of the male. This is similar to what was found with coyotes in Yellowstone Park; that alpha females without betas during period two, were about the den less, and socialized and regurgitated significantly less than did those females with betas. This suggests either that care of pups was passed more intensely to alpha males in packs without betas than to alpha males in packs with betas, or that the pups simply got less attention. Because there was little significant difference between alpha males with betas and alpha males without betas, this backs the latter hypothesis.

Alpha females with betas spent significantly more time at the den, and alone at the den than did the alpha males with betas during period one. However there was no difference during period one between alpha males and alpha females in packs

that had no betas. This suggests that the presence of betas allows the alpha pair to switch roles more than those packs without betas were able to, at least during the first period. This lessens the burden from period to period by allowing the alpha pair to trade in the responsibility of rearing the pups. This is supported by the fact alpha females with betas showed a significant difference in the amount of time they spent present from period to period. Packs with no betas may not have the extra help needed for such a luxury, therefore the help of both parents may be required each period in order to rear healthy pups. Moehlman (1984) found that in golden jackals, with the presence of helpers, the adults spent more time at the den and pups were rarely left unguarded. There was no correlation between the number of betas per pack and the rates of regurgitations from alpha females to pups, which suggests that alpha females without betas were not spending their time away from the den searching only for food for the pups, but rather that they were searching for their own food to help maintain their weight, and the length of their lactation. In fact, as mentioned earlier, during period two, females with betas provisioned the pups significantly more than did those without betas. This is explained in part by the fact that there was a positive correlation between pack size and initial litter size, but the betas helped with feeding the larger packs. Furthermore, in period one, and especially in period two, the graphs (Figures 5-7) showed an increase in the amount of time the alpha female spent at den with each additional beta. The strategies of females with no or few betas in the three periods all indicate that they were spending more time mending costs of reproduction than were those with more betas. The females with fewer betas may have spent more time nursing because the pups were

not getting as much food as those pups that had the betas in the pack to contribute to feedings. Observations of jackal helpers indicated significantly higher rates of regurgitations and/or nursing bouts per hour in families with more adults (Moehlman, 1983).

Alpha females with betas socialized more with their pups than did those alpha females without betas in period two and three. Socializing with the young seems to be an important way of conditioning the pups to interact with other coyotes, and to trigger behaviors associated with their instincts such as pouncing, fighting, and stalking. The capacity of adults to socialize indicates a certain level of health, "free time", and energy. Furthermore, Scott (1967) wrote that the "socialization period" is very important in the development of wolf pups, and stated that "the unique behavior in this period is associated with the formation of emotional attachments to places and individuals." Bekoff (1974) wrote that social play in canids may be necessary for acquisition or elaboration of certain social skills, typical of a species. Furthermore the dominance among pups, which was observed to be established early, may influence who disperses, and who is allowed to stay in the natal territory. The more subordinate pups perhaps being the ones who are forced to disperse early (See Eric Gese 1995). The parents socializing with the young may encourage the play instincts in the pups, thereby helping to establish acts that weed out the weaker pups.

The presence of betas decreased (non-significantly) the amount of time alpha males spent at the den in period one. Since betas spent a lot of time at the den in periods one and two, this may have reduced the time the alpha male needed to

spend at the den. There was a non significant negative correlation (r=-.43, P=0.15) between the number of betas in a pack and the number of regurgitations and the number of whole prey brought to the pups by the alpha male. Therefore the alpha male seems to have had a small decrease in the demand to feed the pups with a larger pack. Furthermore, during period two, alpha males without betas howled significantly more than did alpha males with betas, evidence that they needed to spend more time informing other coyotes of their presence than did those alpha males with betas.

Harrington and Mech (1983) hypothesized that wolf helpers may benefit parents directly through foraging relief, and found that the influence of betas on an alpha female might be indicated by a change in her patterns of attendance about the den. Furthermore, Bennun (1994) wrote in social weavers (Pseudonigrita arnaudi), pairs that were helped may reduce their provisioning effect slightly, not by lowering the rate of feeding visits, but by spending less time searching for food, or by taking the highest quality food for themselves.

Woolfenden (1975) found that scrub jay (Aphelocoma aerulesceus) helpers did not take part in nest building, incubating, or brooding. This is similar to roles played by coyote helpers. All alpha females and alpha males, to some extent, have to reconstruct former dens. The alpha females nurse the young and keep the pups warm during the early part of pups' lives. Those that have no beta helpers have the responsibilities of the above and the sole responsibility of making sure that there is adequate food and protection for the pups. Those with betas must meet certain obligations to rear healthy pups. However, they are able to spread this meeting of

the pups' needs among many members of the pack.

Benefits to the Betas

Cooperation is favored in the evolution of those species which "saturate" their habitat. Low annual mortality rates among yearly resident territorial breeders release few territories for new breeders to establish themselves in each year (Kinnaird, and Grant, 1982). This territorial pattern was found in Yellowstone Park. Consequently there would appear to be many benefits to those betas who stay in their natal territories.

Beta males and beta females followed roughly the same changing of roles between periods one-three as did the alpha pair. Female betas spent significantly more time present at the den than did beta males during period one. This suggests that one reason for the betas to delay their own reproduction, and to stay to help rear their siblings is so that they can learn from their parents how to rear their own young. Female betas learn from alpha females, and male betas from alpha males. Wilson (1975), referring to primates, discusses the fact that young females who handle the young gain experience as mothers before committing themselves to motherhood. He then writes that evidence for this is found in species where allomaternal care is prominent. This "practicing" behavior is displayed by juveniles and subadult females.

There was no statistical difference within period two between how much time beta males and beta females spent at the den; however, males spent more time at

the den during period two than during period one. Females, on the other hand, spent half the time at the den as they did in period one. There was no correlation between the sex of the beta and the rate of regurgitations. During period three both sexes spent little time at the den. During this time, they may have been exploring new territories, or resting and foraging for oncoming winter.

One can establish that as long as the parents of the current offspring were the betas parents, each sibling the beta helped to rear was genetically equivalent to rearing a pup of their own. Another advantage was the betas got a safe environment in which to forage, and needed not put much energy into defending the territory. There have been eight instances where a beta has become an alpha of its natal, or a neighboring territory. In one case the beta male appeared not to be related to the alpha pair it had helped that year. The alpha male was killed by a car. The beta male then became the alpha male of that territory. In another case, a beta female helped her parents, and then disappeared the following year. Some field technicians saw her later several territories down the valley. She was killed, how is unknown, and a necropsy showed placental scars, an indication that she had had young, which suggests that she had gained alpha status. In another case, a daughter helped her parents one year but not the second. The alpha male of her pack (her father) was killed, how is unknown; that same winter the alpha female was seen mating with several males until she settled with one. The female had one pup only and that winter she was killed by a car. Her daughter, who had been returning periodically, took over the territory the following summer with a

mate of her own.

Brown (1983) writes that some of the factors influencing reproductive success are age, experience, environment, group size, and the sharing of a mate. He writes also that all helper-strategies may be regarded as having originated as devices to obtain breeding status, and to obtain mates with the help of other group members. One strategy that Brown mentions helpers may use is the "patient strategy," characterized by a delayed maturity, and a prolonged association of the young with their parents and other relatives. This strategy has an annual survival rate of .8 to .9, when compared with the low survival rate of more "impatient strategies". Helpers observed in Yellowstone Park seemed to have adopted the patient strategy. They may have stayed with their parents for one or two years. Usually they did not attempt to breed. Staying to help in Yellowstone Park seems to have an overwhelming number of benefits, most of which were mentioned earlier. The northern range has a dense population of coyotes, which makes it difficult for the young to disperse successfully to obtain a territory of their own for rearing their young. The food-base during the denning season is reasonably stable and high, so that there will be little competition among pack members. The northern range also is quite close to the border of the Park; therefore, when coyotes disperse they can leave the Park. If free territories are scarce, then they easily could be pushed onto the poorer quality ranchlands outside. Once they leave the Park their chances of survival are low. A number of collars were returned to the coyote study, worn by coyotes that had left Yellowstone Park. In most cases when a collar was retrieved without the coyote, the coyote was dead. Staying in their natal territory, therefore,

may increase their chances of survival greatly. Harrison (1992) hypothesized that juveniles who dispersed may be forced to by siblings or parents, and found that dispersers had a lower rate of survival (.47) than those that stayed in their natal territory (.74). This would indicate that the betas will help to rear their siblings until the siblings reach an age where they could be competition for food or for space in the high quality territory. The betas may drive out the young, a strategy which seemed to take place in Yellowstone Park (See Gese 1995).

There was no correlation between the number of pups in a litter and the rates of provisioning by the betas of a pack, or between the rates of provisioning to the pups and the number of betas in a pack. This suggests that the provisioning of pups by betas was more a process of learning for the betas than it was based on the needs of the individual pups. Furthermore, there was a correlation between the number of regurgitations and bringing of food from the alpha pair and the number of pups in the litter, but was not between the provisioning by the alpha males or betas and the number of pups in the litter. With more pups the alpha females took the responsibility of extra feedings, not the alpha males or the betas. Healthy females could easily have caught enough high quality ground squirrels to feed a larger litter. The betas contribution to the pups seem to be equivalent to that by the alpha male.

Krebs and Davies (1987) show a graphical summary which indicates that the older the beta, the less genetic pay-off he or she will get by staying to help and by delaying his or her own reproduction. This is supported by the fact that there was only one beta known over two. Coyote 848 was eight when he helped. He may have been the father of the breeding female on whose territory he was. It may well

be that there is an optimum age in which to reproduce, and an optimum age in which to help. For example, it may be good to help when one is young and inexperienced, and also, when one is old an unable aggressively to defend the rights to a mate or to a territory. Eight years is old for a male coyote. By helping his daughter, if 840 indeed was his daughter, he still would be getting a "genetic payoff" and a territory where he alone was not responsible for fighting off intruders.

The benefits to betas regardless of their relation to the young, seem to be great. Therefore one would expect to see more helpers that were not related to the young which they provision. This, however, was not the case. Perhaps the alpha pair discourages nonrelated helpers. Reyer (1984), found in Pied kingfishers (*Ceryle rudis*) that secondary helpers (those not related to the breeding pair) were not tolerated around the nest until the young were hatched, unlike related primary helpers. This is an indication that the breeding pair do not trust completely those that are not related. In addition there would be the risk of mate-competition from unrelated male helpers for the alpha female, and from unrelated female helpers for the alpha male. Finally, the alpha pair might prefer to let sons or daughters onto the territory to help, rather than those not related. If these young had survived the first difficult year, it would have been worth allowing them to stay longer to increase survival further. Some betas were present on the territory, but never seen around the den. It is unlikely that they fed or guarded the pups only while they were not being observed. This anomaly of non-helping betas implies that betas who stay on their natal territory do not "pay rent" merely by feeding and guarding the

current young. It suggests that the relationship between the alpha pair and the betas is a complicated one that is fortified by benefits to the alpha pair and to the betas, benefits to the current pups seem to be side results.

Benefits to the Pups:Hypothesis 5

There was a negative correlation between number of betas per pack and the survival rate of the pups. However, in 1992 there was an outbreak of parvo virus which hit packs regardless of size. Furthermore no implants had been placed in one pack without betas, and the second pack without betas that year had no mortality signals in their implants. Therefore, the data from all pups retrieved and receiving necropsies skewed the distribution towards packs with betas. Because of this I do not feel comfortable relying on these data.

Pups in packs with betas had a significantly higher rate of provisioning over the summer than those in packs without betas. Pups with more betas were left alone significantly less than those with fewer or no betas. Bennun (1994) found that breeders did not seem to reduce their feeding rates due to the presence of helpers in social weavers, rather the helpers supplemented their efforts. Millar(1977) writes that a reduction in the size of the offspring would result in a higher metabolic intensity and a smaller energy reserve, therefore smaller offspring may not have the energy reserves required to survive extended periods away from their mother. There was no correlation between the weight of the pups at capture and the size of the pack. This finding relates back to the benefits to the alpha pair from having

betas. Pups in smaller packs are not lighter than pups in larger packs. This may be explained by smaller packs having smaller litters, hence larger pups per litter, and by the alpha female, in packs with no betas, nursing the pups longer to increase their weight.

QUESTIONS RAISED

Long-term pair bonds are reinforced by holding territories year round. Pair bonds also ensure that subsequent litters of pups will be full siblings. The latter has important implications for the kind of selective pressures exerted on some pups to stay and to help to raise the next litter (Moehlman 1983). Harrington and Mech (1983) suggested that in wolf packs the auxiliaries have the opportunity to help, if they remain in their natal territory. This makes helping an ontogenetic epiphenomenon of nondispersal and postponed breeding based on more immediate circumstances. This coyote study supports in part their findings. There appears to have been an environmental pressure, discussed above, for some young not to disperse. The benefit to the alpha pair, from having their pups to help rear the next years litter, appears to be great. Consequently, there may be an undetermined pressure from the alpha pair for the young to stay on. Mech (1970) suggests that in wolves, social factors are very important in regulating pack size. Why do not all coyotes in Yellowstone Park have beta helpers? Though not tested statistically, it did not seem that packs with no betas had poorer quality territories, therefore I would not expect lack of a sufficient food base to cause young to disperse early in those packs. Overall, every member of the pack seemed to gain from the presence of betas. The pups may have been affected the least. The weights of pups in packs with no betas were not different from pups in packs with betas. Furthermore, though pups were left alone more in packs with betas, there was not a high rate of predation on any pups. Benefits, or costs, to the pups, from the presence of betas, may be

clearer in the future. Pups in packs with betas were socialized with more than those in packs without betas. If this socialization is important for survival, then once dispersed, a difference in the health of pups may be observed. If betas do force subordinant pups to disperse, then it may be to the pups' advantage to be reared in a pack with no betas, especially if the alpha female nurses the pups more to make up for the lack of extra feedings. Then, the only competition for staying in the natal territory would be with littermates. One could argue the presence of the betas selects for stronger pups that have a better chance of survival. Pups that could compete with the betas must be healthy.

Are the benefits of having beta helpers at the den enough to encourage coyotes to form packs larger than the alpha pair, or is helping during the denning season a side benefit to packs formed for other reasons? Why does not every pack have beta helpers? Why do not all the betas help to rear the young? Why are they tolerated on the territory if they do not help, or do they help in some indirect way? Perhaps there is an optimum size for a coyote pack in an area such as Yellowstone Park. For example too many betas in a pack may increase the competition between the alpha pair and the betas, and between the pups and the betas. Too few betas decreased the amount of time the pups are guarded, the amount of food they received, and increased the amount of time the alpha pair spent on behaviors related to the survival of the pups. However, in an area with a low food base during the denning season, or where remaining unseen would be important for survival, one would expect packs to be smaller.

A study similar to this would benefit from being of longer term. Following the young when they disperse, and measuring the long-term rate of survival and of reproductive rate of betas that helped and then dispersed would be of great value when compared with the betas that did not help and dispersed. Studying in depth which betas stay and help and which do not, and why, would be interesting. It is known that most of the betas that did not help were related to the alpha pair. Therefore it is not a case of betas related to the pups being tolerated around the den, and those not related to the pups not tolerated. Another important component to a future study would be to see if there were a correlation between the number of betas in a pack, and the rate of survival of the alpha pair (and the number of betas compared with the tightness of a pack). For example, do alpha pairs with no or few betas stay together for a shorter period than do those that have more betas and therefore, have less of a solid pack structure? Finally, only twelve coyote packs were studied in depth, which decreased the sample size, but which increased the knowledge of the workings of each pack. However, having a bigger sample size, and an in depth study would increase the significance of the results dramatically. This, no doubt, would give greater confidence to those presenting the study in regard to its implications.

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APPENDIX

Betas Defense of the pups

On several occasions, a beta helped to defend a den from a potential predator. However, there were not enough instances to test statistically. In one case, a Grizzly sow and her two cubs were observed 100 m from the den. It appeared that the bear had stolen an elk calf the pack had killed. The pack surrounded the grizzly, barked and circled her until she left with her cubs. In another case, a grizzly came within 150 m of the den and the alpha male, female, and all betas, circled the grizzly lunging at her periodically. Betas also were observed helping the pack to chase out coyote intruders. Ravens too were chased away, particularly when the pups were young. In one case, a field technician observed a lone beta while a raven dived towards the den. The beta chased the raven and appeared to try to catch it. The beta then sat over the entrance to the den while the raven circled overhead. Sixteen ravens then joined the first and the beta moved into the den, so only his head was sticking out. The beta had his ears back with an aggressive facial expression. After forty minutes of plugging the den entrance, the beta chased the ravens and again returned to sitting in the den entrance. This continued until the ravens left finally. The adults of different packs would spend hours hunting and traveling about the territory with badgers. Its presence did not seem to bother the coyotes. This may support Minta et al (1992) findings that coyotes which spent time with badgers ate prey at higher rates than did those which did not spend time with badgers. Finally, if people came too close to a den, betas would bark and howl, which usually caused the pups to return to the den.