Wild and Captive Wolf (*Canis lupus*) Aggression In Relation to Pack Size and Territory Availability

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Abstract

Concern has been expressed that captive wolves (*Canis lupus*) are more aggressive toward pack-mates than wild wolves. Higher aggression in captivity could be detrimental to the animals' health and human safety. This study compared average aggressive behaviors displayed per hour in wild and captive packs. The 11 captive wolf packs that were observed exhibited an average aggression level four times higher than a wild pack in Yellowstone National Park (22.52 and 5.13, respectively). For the captive packs, I focused on the relationship between intra-specific aggression and the size of the enclosure, area available per wolf, and number of wolves per enclosure. Previous research suggested that a subordinate wolf might only escape the aggressive displays of a dominant wolf by fleeing a given distance. The territory size, as measured by area of the enclosure and area available per wolf, is an indication of the distance a subordinate wolf can retreat. Contrary to expectations, only a slight logarithmic relationship was found for the effect of territory size on intra-pack aggression. The number of wolves in a pack, however, had a significant and positive correlation to aggression level (R^2=0.7303; Sig.F=0.0016). This points toward the importance of social factors, such as relatedness, age, hybridization, resource competition and stability of the pack, in the cause of higher aggression in captive wolves than in wild wolves. With further research, these results could be applied while planning enclosure design, resource allocation and reintroduction and captive breeding efforts for wolves and possibly other socially hierarchical species.

Introduction

Due to an ever-increasing demand for wolves (*Canis lupus*) as pets, the captive wolf and wolf-dog hybrid population is exploding. In 1994 there were an estimated 500,000 wolves and hybrids living in captivity in the United States, while less than 2,000 wolves remained in the wilds of the lower 48 states (Hope 1994). Today, the number of pet wolves and hybrids is far greater, with breeders spreading across the world and the popularity of the wolf at an all time high. Every year, over 250,000 new pups are sold to Americans (Gibson 1996).

The unpredictable nature of wolves and hybrids has led to many of the pets ending up homeless within three years. Seventy-five percent do not survive their first year because of human abuse, neglect, or accident (Gibson 1996). As pups, nearly all wolves and hybrids behave like docile dogs, readily playful and relatively submissive. However, as they grow and approach sexual maturity, most become predatory, wide-ranging, highly territorial, and pack-oriented animals (Hope 1994, Klinghammer 1987; Rabb et. al. 1967). Commonly, the previously adopted pup challenges the dominant householder through warning growls and bites, much as it would in a wild pack. Though the wolf or hybrid does not intend injury, a human is much more vulnerable to attack than a socially adapted, heavily coated wolf. As a consequence of

their wolf-like characteristics, for which they were originally purchased, pet wolves and hybrids are very often left without a suitable home.

In response to the problems facing these homeless wolves, shelters and refuges have opened to take in and care for them. The people who run the shelters dedicate themselves to preserving the health and wellbeing of as many of these animals as possible. This requires detailed knowledge of wolf and hybrid behavior in order to provide for their physical and psychological needs. Observations and research into wolf social organization, particularly levels of aggression, are important in providing the caretakers with information to ensure the wolves and hybrids' health and the safety of visitors. My goals in this study were to address these issues by providing some insight into the causes of aggression in captive wolves.

Wild Wolf Social Organization

An understanding of the social organization of wolf packs is necessary in order to address the needs of captive wolves and hybrids while assuring the safety of humans. The wolf is a social animal. Wild wolves typically live in packs varying in size from 2 to 15 individuals in the continental United States, and may congregate in packs much larger in Canada and Alaska (Landau 1993). A pack is typically composed of a breeding pair of wolves, known as the alphas, their young pups, and their offspring from earlier years (Haber 1977; Murie 1944). There are four categories of wolves in a well-

established pack: (1) the alpha pair; (2) mature subordinate adults; (3) omega or outcast wolves that live on the periphery of the pack's social core; (4) and juveniles that haven't reached sexual maturity and have not entered the pack's social center (Woolpy 1968). Males and females have separate hierarchies, and each are reluctant to interfere with the affairs of the other sex (Derix et al. 1993; Derix et al. 1995; Rabb et al. 1967). For both of the sexes, as wolves move down the hierarchy, individuals are more submissive and have to work harder for their food and social acceptance (McLeod 1997; Olson 1938).

The dominance of an alpha male or female is created by the nature of an adult's dominance over its progeny. As the breeders, the alpha pair is the leader of a pack consisting primarily of their offspring. Alpha wolves are responsible for the leadership of their family (Clark 1971; Mech 1970, 1988, 1999; Young and Goldman 1944). They initiate hunting trips, maintain order and accord in the pack, and are the primary caregivers for the pups. Subordinate adults rarely challenge the dominance of the alphas, and pups almost universally defer to adults and older siblings. In the wild, dominance displays and intraspecific aggression are infrequent except in competition for food and mates (Mech 1999).

Captive Wolves and Hybrids

Captive wolves and hybrids typically maintain a stricter hierarchy within the pack than do wild wolves (Frank and Frank 1982). It is enforced with more frequent intraspecific aggression and dominance displays (Fox 1972; Klinghammer 1987; Rabb et al. 1967; Schenkel 1967; Zimen 1975). This distinction has been associated with the difference in social bonds between related and unrelated wolves and hybrids (Mech 1999). The majority of captive wolf packs consist of unrelated individuals that did not mature with their present pack mates and companions. Woolpy and Ginsberg (1967) found that up until nine weeks of age, a wolf pup could quickly establish a relationship with another wolf or human. After that point however, socialization becomes increasingly difficult and requires progressively more time. At seven months, when wild pups begin traveling with the pack, their ability to form new psychological ties effectively disappears. Since refuges do not normally obtain the failed pet wolves and hybrids until 1 or 2 years of age, unrelated and relatively unsocialized packs are created. Without the family structure of the basic wild wolf pack to enforce dominance, the wolves and hybrids are left to aggressive behaviors and displays to implement the hierarchy (Mech 1993, 1999).

Many other studies have been done on captive wolves due to their accessibility. Some have focused on health care, management, and early socialization of captive wolves (Klinghammer 1987; Klinghammer &

Goodman 1987), while others looked at vocalizations and how to design enclosures for research possibilities (Schassburger 1982, 1987). Aguilera (1977) and Altmann (1987) touched on the ideas of social interactions between pack members, focusing on overall pack structure. Harrington (1987) studied the use of howling as an aggressive posture in wild wolves. Another study found a correlation between urinary cortisol levels, the amount of aggressive pressure an individual was under, and a wolf's status in a captive pack (McLeod et al. 1995; Moger et al. 1998). Recently, a study compared the activity levels of wolves in small and large enclosures; no significant difference was found between the two (Kreeger et al. 1996). However, these and other studies have not specifically addressed the effect of enclosure size or pack social dynamics on aggressive behaviors.

Intraspecific Aggression

Although recent studies have discussed the possibility that stress and aggression levels are higher in captivity than in the wild (Fox 1972; Klinghammer 1987; McLeod et al. 1995; Mech 1970, 1993, 1999; Moger et al. 1998; Rabb et al. 1967; Schenkel 1967; Zimen 1975), no one has addressed the physical causes of this phenomena. Assuming that the physical environment, such as enclosure size, has an effect on aggressive behaviors in a captive wolf and hybrid pack, a study detailing that relationship could have many methodological, practical, and theoretical implications. Information on

the optimum environment for safety and stability in the pack could improve the quality of life for captive wolves and hybrids and increase the safety factor for personnel working with the wolves. Through understanding and minimizing the impetus for heightened aggression levels, it may be possible to reduce the need for staff to come into direct contact with the wolves or hybrids to separate individuals or attend to injuries. Likewise, such information could be generalized to increase the success of captive breeding programs for the Mexican gray wolf (*C. lupus baileyii*) and the red wolf (*C. rufus*), both of which are seriously endangered. A guideline for the optimal environment for a captive pack could also be used in gray wolf reintroduction efforts that employ a 'soft release' tactic where the reintroduced animals are held in acclimation pens previous to release for familiarization with the area and each other.

Captive wolf and hybrid caretakers have noticed that tensions among pack members escalate to a point of excessive aggression if there is not enough room for the subordinate to escape the pursuits of the dominant aggressor (Fentress 1967). This restriction in the distance a wolf can flee from its aggressor can be broken down into three variables: the total area of the enclosure, the area available per wolf, and the number of wolves living within an enclosure.

Through studying the relationships between aggression and the area available per wolf, the total area of the enclosure, and the number of wolves

per enclosure, this study was designed to discriminate between their effects, and rank their significance. My goal was to develop guidelines for the minimum space needed per wolf and the maximum number of wolves in a pack in order to promote a healthy and safe environment.

In studying the behavioral interactions of 11 captive wolf and hybrid packs housed in different sized enclosures and 1 wild wolf pack with unlimited area, I addressed the relationships between intra-specific aggression and available area. If aggression is dependent on the area available per wolf, total area available or the number of wolves per enclosure, then aggression rates will change as each of these factors vary.

Materials and Methods

Locations

The first phase of the study took place at Mission:Wolf, a sanctuary in the Wet and Sangre de Cristo mountain ranges of Southern Colorado (9,200 ft. elevation). Mission:Wolf provides for 36 captive born timber wolves and wolf-dog hybrids. The wolves and hybrids had been divided into 15 separate packs in enclosures that vary in size from 0.50 acres up to 13 acres as shown in Figure 1. This sanctuary is set up as a non-profit agency staffed by the founder, Kent Weber, his family, and regular volunteers who live in close contact with the canids.

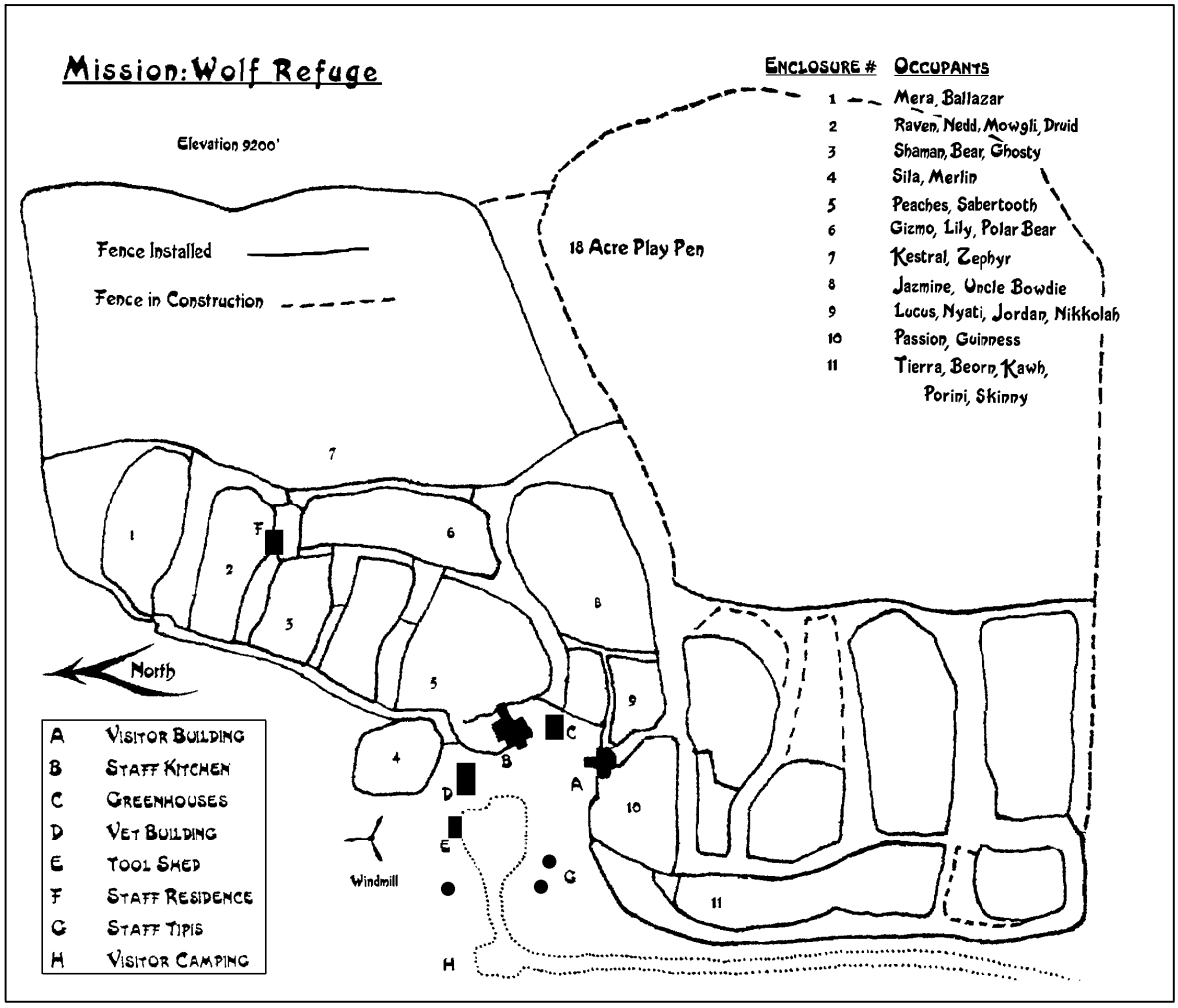


Figure 1. Map of enclosures and building layout at Mission:Wolf.

In order to compare the level of aggression and stress of captive wolves and hybrids to wild wolves, the second portion was conducted in the Lamar River valley of Yellowstone National Park's northern range (Wyoming and Montana). The Druid Peak pack's range spreads from the Absaroka Mountain Range on the Northeastern park boundary in heavy timber and rocky canyons, to the open fields just east of Slough Creek. It spans from the border of Pelican valley to the south into the Beartooth Mountains in the

north (from 6,500 to 11,000 ft. elevations). Druid Peak pack territory is confined to 128,989 acres (522 km^2) (USFWS 1999) by the surrounding Rose Creek and Crystal Creek wolf packs through inter-pack competition and aggression. These three pack territories are highlighted in green, pink and blue respectively in Figure 2.

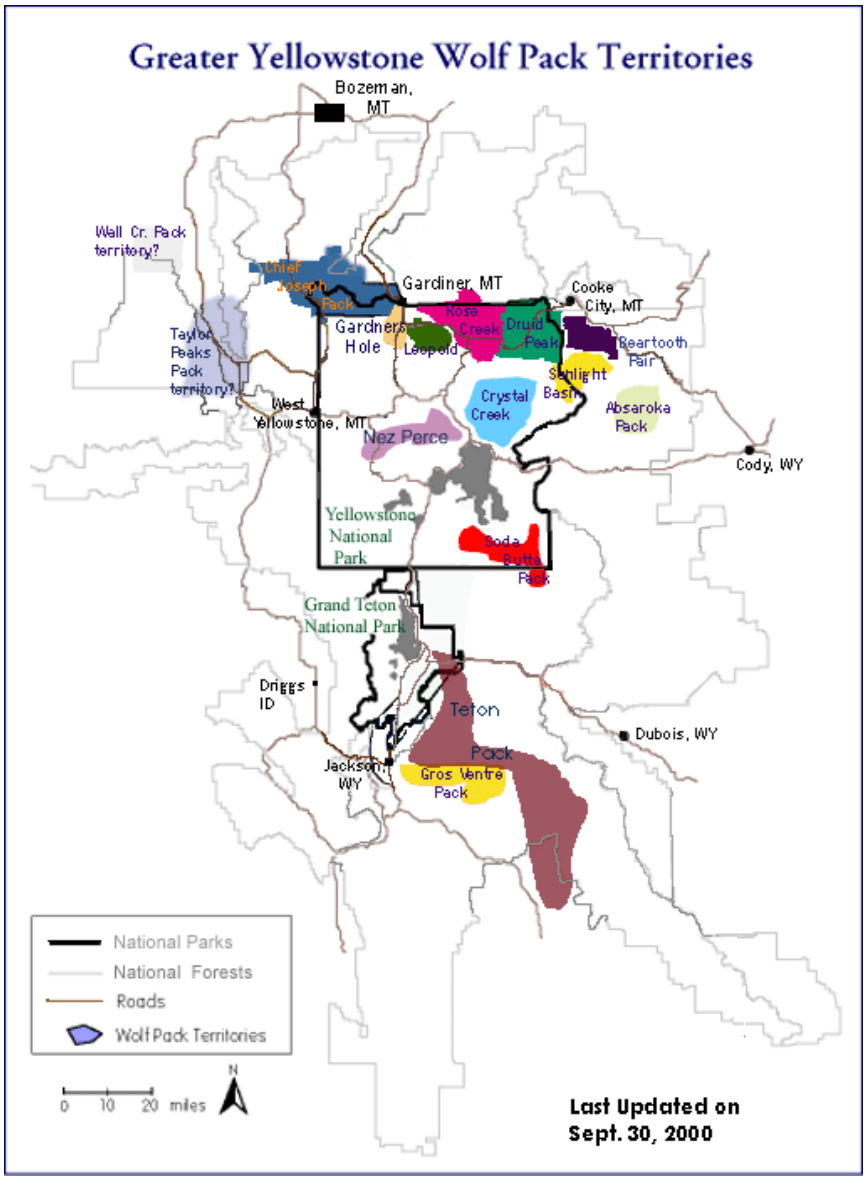


Figure 2. Area map of the Greater Yellowstone wolf pack territories during the summer of 2000. The Druid Peak pack's territory is highlighted in green. Territory size and location is determined through reported sightings and radio collar signal locations.

The Canids

Thirty-one captive wolves and hybrids were observed at Mission:Wolf for the study. Starting in 1993 all of the males were given vasectomies in order to prevent unwanted litters, while leaving their hormonal levels and natural behaviors intact. As each individual arrived at the refuge, they were either given a name or kept the name from their previous owners. For simplicity's sake, each wolf or hybrid was referred to by name for the duration of the study (Table 2). Of the 31 individuals, 29 are thought to be full-blooded wolves; only Dancin' Bear and Ghosty are wolf-dog hybrids. Their ages range from 6 to 14 years old. Of the 31 animals observed, 13 were female and 18 were male. The 31 canids are divided into 11 packs, varying from 2 to 5 individuals.

For the wild wolf section of the study, I observed the Druid Peak Pack of Yellowstone National Park during the summer of 2000. As a part of the Northern Rockies gray wolf reintroduction effort, 31 wolves were released into the park in 1995 and 1996. Each pack was initially kept in acclimation pens in the backcountry for three months, in order to promote pair bonding and adjustment to their new habitat (Smith 1995; USFWS 1994). The Druid Peak pack was released into the wild with 5 members: M38, F39, F40, F41, and F42. In the numbering system, the "M" and "F" stand for male and female while the actual number refers to the order in which the individual wolf was collared. Since 1996, many changes have occurred in the

composition of the pack. In the summer of 2000, the pack consisted of M21, F42, F103, F105, F106, an uncollared gray male yearling, an unidentified gray male adult, and 20 pups of the year. Though it is unusual for a wild pack to have so many members, pups that do not typically participate in the social order were the majority. (McLeod 1997; Zimen 1981).

Behavior Descriptions

The designation of types of aggressive behaviors that were studied was conducted at Mission:Wolf on the captive wolves and hybrids before the actual study began. By first observing and then recording the frequency and duration of any apparently aggressive behaviors, an ethogram was created, consisting of growling, biting, chasing, and pinning. This ethogram is shown below:

Table 1. Ethogram of measured aggressive behaviors

Bite	close jaws and teeth on another, may or may not wound
Growl	a throaty rumbling vocalization usually of low pitch
Chase	running pursuit with frightened and submissive behaviors during or after, by the chased wolf
Pin	lunge and bite at the neck, muzzle, or body of another wolf , forcing it to the ground and holding it there

In recording and analyzing the data, it was decided that 1 second of growling or chasing would be counted as one unit of behavior, in order to quantify the behavior's intensity. One-second intervals were appropriate for this study

because of the moderately consistent low numbers of aggressive behaviors initially observed. Only the frequency of biting and pinning were recorded because these behaviors were not dependent on duration for their force.

Captive Observations

The data was collected between October 1999 and February 2001. A total of 67 hours were spent watching different packs. Observations were restricted to the early morning (5:00 to 8:00 a.m.) and early evening (5:00 to 7:00 p.m.) in order to observe the wolves when they were most active.

I used a focal behavioral sampling method because distinct variables, separate packs, and one particular category of behavior were studied. Observations focused on all of the behaviors of one pack of wolves for a specific time interval. The open terrain in and around the enclosures at Mission:Wolf, as illustrated in Figure 3, allowed for consistent viewing of all members of a pack. Due to the high visibility of the wolves and hybrids studied, aggressive behaviors of every individual in the pack was continuously recorded. During this phase of the study, two research assistants and I observed specific packs for one-hour intervals and recorded any aggressive behaviors. The person watching a particular pack for each hour was randomly determined, so as to eliminate observer bias. To control the potential effect of human presence on a pack's behavior, no one pack was given more acclimation time to the observer than the others.

Figure 3. The open terrain in and around the enclosures at Mission:Wolf made it possible to consistently observe all members of a pack for one-hour intervals.

Data recording stopped during particular instances that could have affected the canids' behavior as all 11 packs could not be monitored simultaneously. For instance, behaviors were not recorded directly before, during, or after feeding, because tensions greatly increased between packmates, exponentially affecting aggressive behavior rates. Whenever a visitor or group of visitors approached one of the enclosures, we would stop observation because the wolves and hybrids would either shy away from the person and each other or they would confront the intruder. Finally, observations needed to pause whenever the staff was particularly active because the wolves and hybrids would become excited.

Wild Observations

The Druid Peak pack was observed between August 6, 2000 and August 25, 2000 for a total of 91 hours. Observation generally occurred between 6:00 to 10:00 a.m. and 6:00 to 9:00 p.m. due to higher activity levels and pack visibility. During the late summer, wolf pups are old enough to leave the den; however, they do not have the stamina to travel with the pack during long treks or while hunting (Mech 1970). Therefore, the pups are left at a rendezvous site with an adult "babysitter" while the rest of the pack patrols the territory (Wynne-Edwards 1962). In the case of the Druid Peak pack, the rendezvous site was located in the middle of the Lamar Valley, approximately a mile south and west of the Lamar River confluence (Figure 4). Due to the nature of the terrain, the pups were visible most of the day and the comings and goings of the adults were conspicuous as shown in Figure 5. It was also possible to watch the activities of the adults for much of the time because they frequented other open areas of the valley.

Once individuals could be identified by distinct markings, it was possible to use focal behavioral sampling for aggressive behaviors. There were times when the whole pack was not visible; however, it can be assumed that few aggressive behaviors were missed because most social interaction in a wild wolf pack occurs at the den and rendezvous site during greetings and feedings of the pups (Fox 1972; Mech 1970; Murie 1944).

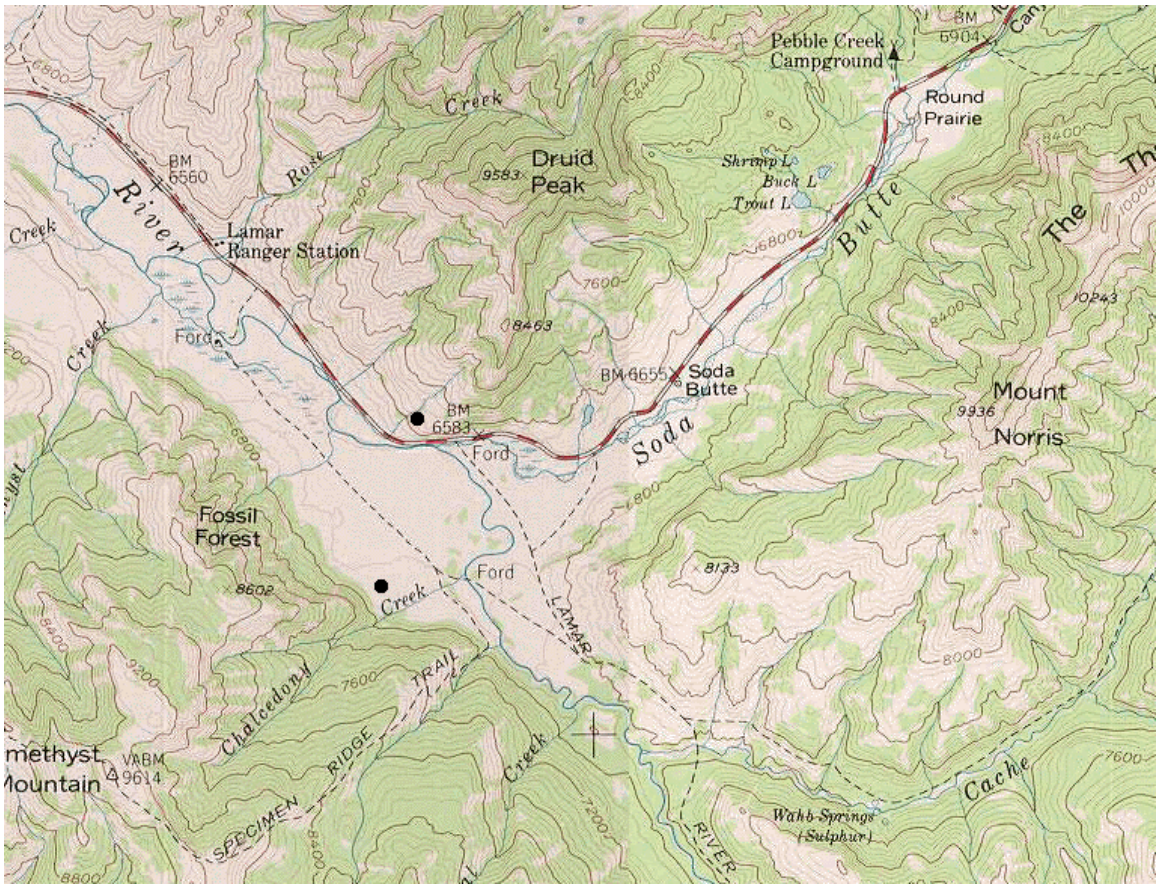


Figure 4. Topographic map of Lamar Valley and surrounding areas, encompassing most of the Druid Peak pack's territory. The upper circle indicates the main point from which observations were made. The lower circle indicates the rendezvous site for summer 2000.

Figure 5. Rendezvous site of the Druid Peak pack during the summer of 2000 in the Lamar Valley, taken from the main observation point.

I employed several methods for locating and observing the wolves. For the majority of the time, the wolves were approximately 0.50 to 0.75 miles away from the observers, so a 16-47 x 60mm waterproof Spotter XL spotting scope was used. In order to help identify and locate individuals, both radio tracking and airplane spotting were utilized. Five of the seven adult wolves, M21, F42, F103, F105, and F106, are fitted with radio collars (previously attached by US Fish and Wildlife Service) that transmit on unique frequencies, allowing researchers to track their movements with a hand-held receiver. The National Park Service also conducts weekly fly-by surveys of the wolves in the park. During flights, the pilot was in direct communication with other biologists and researchers on the ground, including myself, all working together to get an accurate count and location of the wolf packs. By using the hand-held radio receivers, it was also possible to follow the Druid Peak pack either along the road or into the backcountry by foot. During the study, it was common to have one person stationed at the Lamar River confluence watching the rendezvous site while other researchers were searching other areas of the Lamar Valley, Little America, and Specimen Ridge for the rest of the pack. In one instance it was necessary to hike 7 miles into the backcountry, along the Cache Creek trail and South Cache Creek trail, to locate the pack.

Statistical Analysis

As was stated previously, one second of growling or chasing was counted as one unit of behavior and each pin and bite were counted separately. The occurrence of each behavior and the total aggressive behaviors for each pack was divided by the number of hours each was watched, thus coming up with the values for "aggressive behaviors per hour." Then, it was necessary to ascertain the areas of each enclosure at Mission:Wolf from a map of the refuge. In order to determine the "area available per wolf", the enclosure size was divided by the number of wolves held in each pen.

To serve as a baseline for natural aggression levels, the "aggressive behaviors per hour" were calculated for the Druid Peak wolves. By comparing these data to the captive aggression data, it is possible to demonstrate the relationship between captivity and aggression. The pack's large territory size (128,898 acres) can be considered essentially unlimited because a member may disperse from the pack at any time.

Results

To effectively examine the effects of environmental factors on captive wolf and hybrid aggression, I tested whether there was a difference in aggression level between wild and captive animals. The mean of the

aggressive behaviors per hour was found for the 11 captive packs: 22.52+/- 0.07. This was then compared with the measured value of wild aggressive behaviors per hour: 5.13 (Table 2). Since the wild mean does not fall within the standard deviation of the captive mean, there is a significant difference between wild and captive wolf and hybrid aggression levels. In fact, the captive wolf and hybrid aggression rate was approximately four times that of wild wolves, as is illustrated in Figure 6.

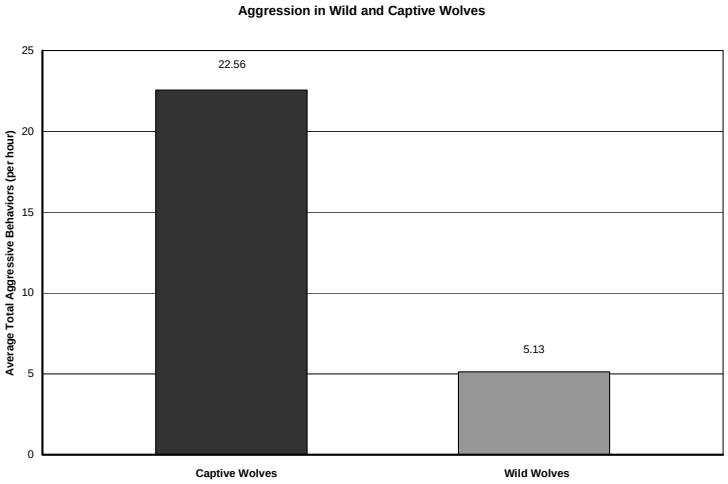


Figure 6. Captive aggression levels are approximately 4x higher than wild aggression levels.

When considering only the captive packs, regression analyses were conducted to determine the relationship between the aggressive behaviors per hour and the three measures of environmental factors: total area of enclosure, area available per wolf, and the number of wolves per enclosure.

Neither the total area of the enclosure nor the area available per wolf had a significant effect on aggression level (R^2=0.0111; Sig.F=0.7720; Figure 7; R^2=0.0296; Sig.F=0.6345; Figure 8; respectively). However, when the outlying data points (pack #1 for aggression and pack #9 for area – as referred to in Table 2) were removed, a slight logarithmic function can be

detected for both. It is noteworthy that these two factors apparently play a similar, yet minor role in aggression levels in captive wolves and hybrids.

Figure 7. Logarithmic effect of total area of enclosure on captive aggression level.

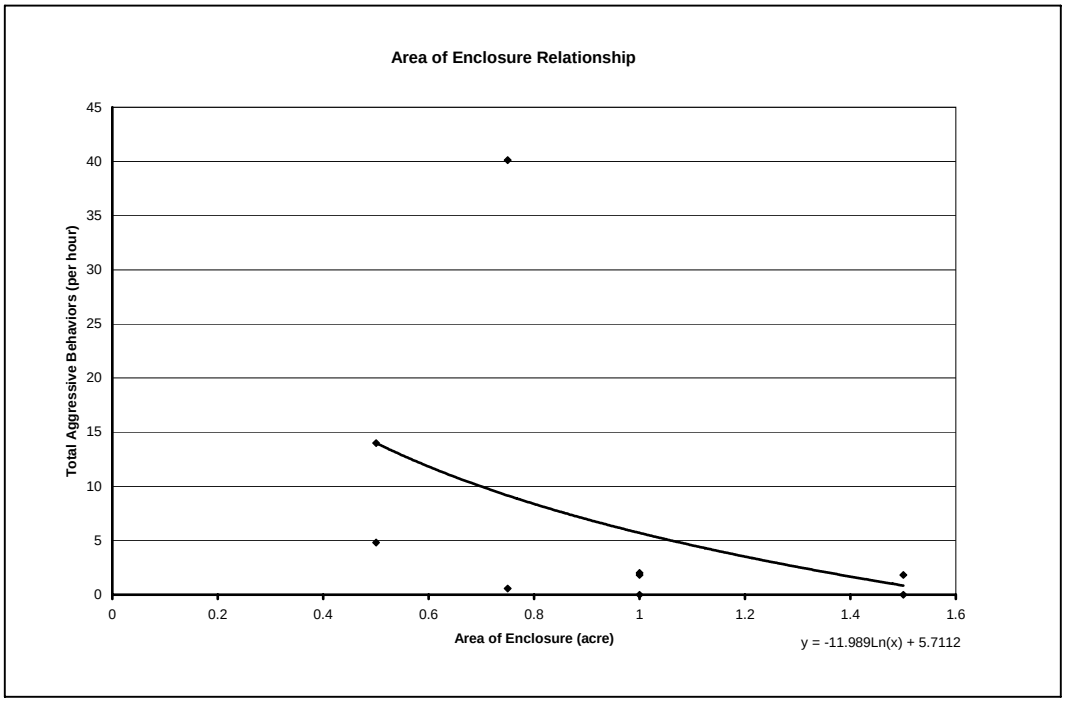


Figure 8. The relationship between area available per wolf and aggression in captive packs.

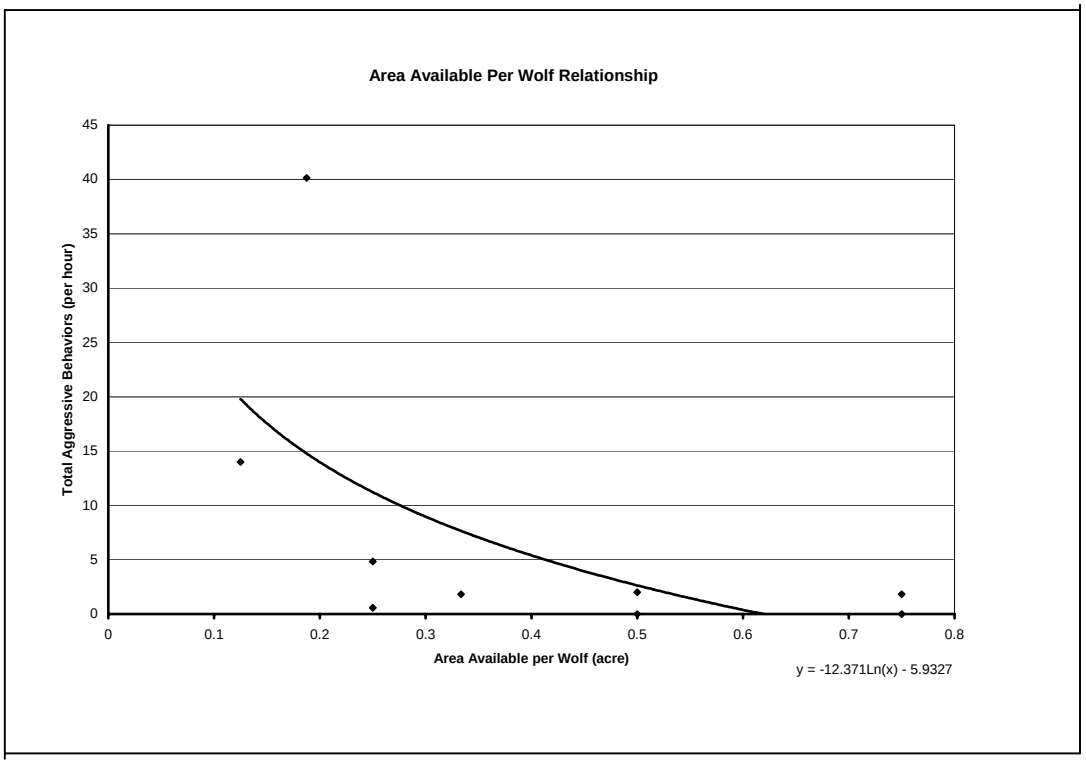
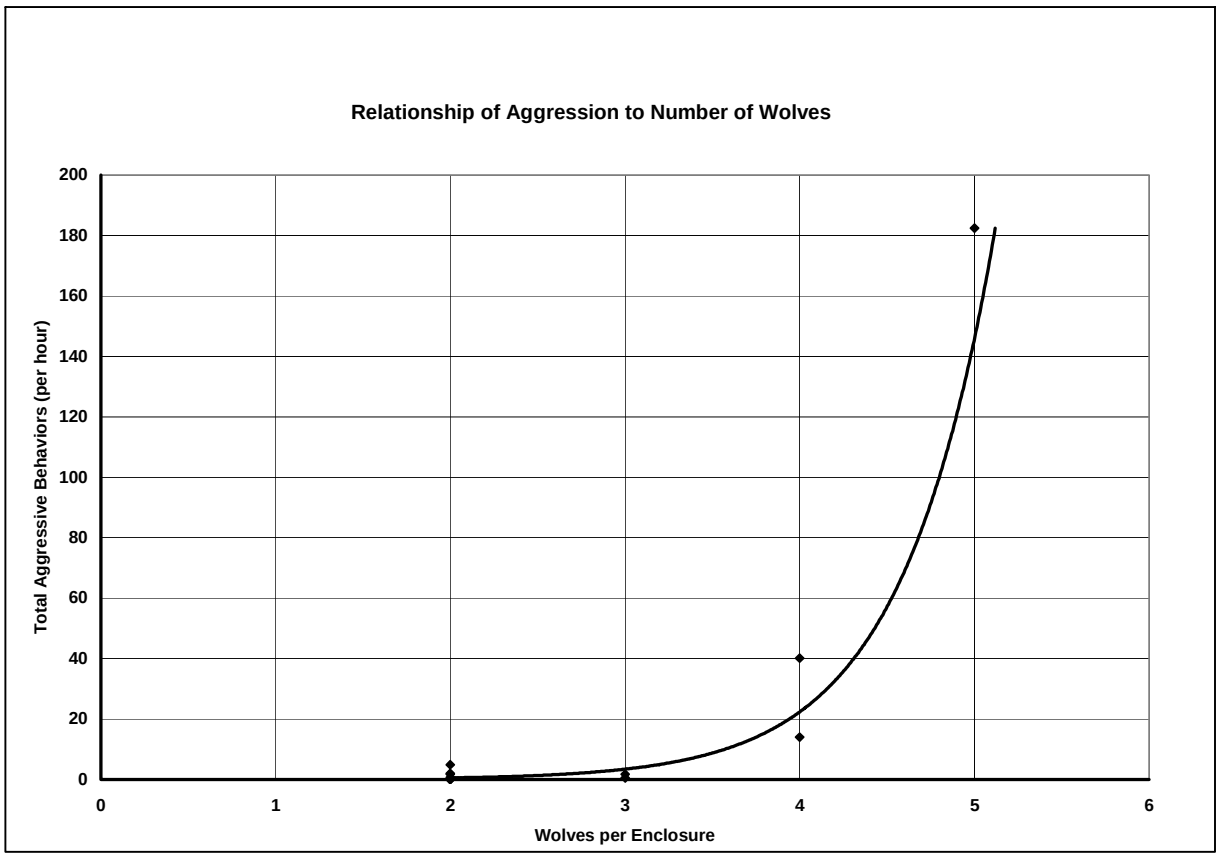


Table 2. Compiled data for captive and wild packs at Mission:Wolf and Yellowstone National Park.

	Enclosure	Area of pen (acre)	Avg. area per wolf (acre)	Hours watched	Growls per hour	Bites per hour	Chases per hour	Pins per hour	Total agg. beh. per hour	Wolves per pen
Captive Wolves	**1. Kawh, Tierra, Porini, Skinny, Beorn**	1.50	0.30	5	24.00	13.60	142.80	2.00	182.40	5
	2. Raven, Mowgli, Druid, Nedd	0.75	0.19	8	23.88	1.38	9.00	5.88	40.13	4
	3. Lucus, Jordan, Nikkolah, Nyati	0.50	0.13	8	9.75	0.75	2.25	1.25	14.00	4
	4. Polar Bear, Gizmo, Lilly	1.00	0.33	6	1.67	0	0	0.17	1.83	3
	5. Shaman, Dancin' Bear, Ghosty	0.75	0.25	7	0.43	0	0	0.14	0.57	3
	6. Merlin, Sila	0.50	0.25	6	3.00	0	1.33	0.50	4.83	2
	7. Passion, Guinness	1.00	0.50	6	0.67	0	1.33	0	2.00	2
	8. Peaches, Sabertooth	1.50	0.75	6	1.33	0	0.33	0.17	1.83	2
	9. Zephyr, Kestral	13.00	6.50	8	0	0.38	0	0.25	0.625	2
	10. Uncle Bowdie, Jazmine	1.50	0.75	4	0	0	0	0	0	2
	11. Ballazar, Mera	1.00	0.50	3	0	0	0	0	0	2
Wild	**12. Druid Peak ***	128,989.0	4,777.37	91	0.22	0.14	2.80	1.97	5.13	27

The third factor measured in this study, the number of wolves per enclosure, expressed a strong, positive, statistically significant association with levels of aggression in captive wolves and hybrids (R^2=0.7303; Sig.F=0.0016; Figure 9). The correlation is markedly high and there may be an exponential or logarithmic relationship between the two. When the "total aggressive behaviors per hour" is broken down into its components – biting, pinning, chasing, and growling – all four have a statistically significant relationship with the number of wolves per enclosure (bite – R^2=0.6520; Sig.F=0.0047; pin – R^2=0.4418; Sig.F=0.0360; chase – R^2=0.6258; Sig.F=0.0064; growl – R^2=0.8020; Sig.F=0.0005).

Figure 9. The effects of the number of wolves on aggression levels in captive packs.



To serve as a control for observer bias and data skew, a final test was run on the correlation between the number of hours watched and the number of aggressive behaviors per hour. This was necessary because the 11 captive packs were observed for different total amounts of time, possibly allowing the wolves and hybrids in certain packs to become more acclimated to human presence. If acclimation occurred, then it would allow the longer observed wolves to act more naturally than another, less watched pack. However, the regression test showed that there was no such a relationship (R^2=0.0088; Sig.F=0.7969).

Discussion

Baseline Aggression Levels

The aggression level in Mission:Wolf's captive packs was significantly higher than that of the wild Druid Peak pack. These findings are consistent with the traditional idea that captive wolf and hybrid packs are more intra-specifically aggressive than wild packs. In the past, this idea has been extrapolated from different concepts of wild and captive social organization. Retrospective comparisons between studies of wild and captive packs have been conducted, allowing many to postulate that the differing environments and social organizations could cause captive wolves and hybrids to be more aggressive toward one another (Klinghammer 1987; McLeod et al. 1995; Mech 1970, 1993, 1999; Moger et al. 1998).

While the study supports previous speculation, more research must be done before any solid conclusions may be drawn. During the time span in which the study was conducted, the Druid Peak pack experienced many unusual circumstances that have not before been observed in the wild. Three months before the study began, the Druid Peak pack's previous alpha female, F40, was most likely killed by her own pack mates. It is likely that the social hierarchy typically established by parentage in a wild pack was still in upheaval in August, causing an increase in aggressive behaviors aimed at the subordinate wolves.

After F40 was killed, her sister, F42, assumed the role of alpha female and adopted the pups from F40's, F105's and possibly F106's litters. Consequently, there were 20 pups of the year, for which only 6 adults had to attend and feed. There has not been a documented case of another wild wolf pack successfully raising such a large number of pups. Most of the adults' time was occupied with hunting during the study period because elk, their main prey base, were scattered in the high country due to a severe dry season. The adults may have spent less time than usual in aggressive and other social interactions in order to provide enough meat to feed the pups. The presence of pups could have also lowered the observed aggression levels in the adults because an endorphin is released in a wolf's brain while there are pups in the pack that stimulates amiability and playfulness (McLeod 1997). Thus, continued study of wild wolf packs under different social and

seasonal conditions in order to establish a more robust baseline for aggressive behavior levels would be very useful.

There are many thoughts as to why captive aggression may be higher than wild aggression. The remainder of this particular study focuses on analyzing these proposals, as well as their implications.

Enclosure Size

One such proposal, as put forth by Fentress (1967), is that the amount of space a wolf pack has could be a factor in the stress on social relationships. Contrary to expectation, the results of this study do not strongly support the hypothesis that a smaller area available for a subordinate wolf to flee from an aggressor would cause an increase in aggression levels in captive packs. There is a trend that suggests such a relationship in both the area available per wolf and the total area of the enclosure, however it is not statistically significant. If the outlying data are removed (Pack's #1 and #9 in Table 2), then a slight logarithmic relationship emerges between area and aggression. This strongly supports the need for more observation on packs with more variable enclosure sizes, as the small sample size and the clustering of data in a small range limits ability to compensate for individual variation between the packs.

According to Kreeger et al. (1996), captive wolves do not alter their overall activity level in relation to the size of their enclosure. Therefore, it

should not be surprising that their aggression level only varies slightly as the area decreases. This could imply that even if the enclosures are large enough to mitigate aggression, the strong social bonds that form the pack hold the members in close contact.

This is evidenced by the omega's reluctance to leave the pack. In both the wild and in captivity all other members of the pack dominate the omega wolf whenever a frustration or conflict arises. The omega is considered an outcast that is typically not allowed to eat until the rest of the pack is finished. Yet, despite these difficulties, an omega wolf prefers to remain on the fringes of the pack than to disperse (Messier 1985; Wynne-Edwards 1962). There have been cases where an omega was removed from an enclosure due to a high risk of injury from aggressive dominance by other pack members. In most of these cases, the removed omega will go to great lengths to rejoin the abusive pack. When the omega is not allowed to rejoin the pack, they will usually become lethargic, stop eating and show signs of depression (White 2001). Consequently, separating an omega from its pack is only beneficial when the situation is dire. Wild omega behavior corresponds with captive experiences. A wild omega will remain physically close to the pack through repetitive rebuffs and molestation (Messier 1985). Only when death or severe injury is imminent will the omega leave the pack (Rabb et al. 1967; Shenkel 1967). Seemingly, an omega will only flee from an aggressor to

a significant distance when it finally disperses, an option that is not voluntarily possible in captivity.

Number of Wolves

The study found a strong relationship between the number of wolves in an enclosure and the aggression levels of captive wolves. This supports previous studies that pack social order becomes more complex and therefor more volatile as the number of wolves in a pack increases (Mech 1970; Olson 1938; Woolpy and Ginsberg 1967; Zimen 1976). As pack size increases, there is an inherent rise in competition for resources. This causes an increase in the need for aggression to be used as a tool in implementing the social hierarchy.

With more study, either a logarithmic or exponential relationship may emerge. Interestingly, there are strong relationships and correlations between the number of wolves in an enclosure and the four different aggressive behavior types: bite, pin, chase and growl ($R^2 = 0.4418$; $R^2 = 0.6258$; $R^2 = 0.6520$; $R^2 = 0.8020$, respectively). This increases the validity of the claim that the number of wolves in, and thus the social complexity of, a pack has a significant effect on aggression. Such a strong, positive correlation suggests that wild packs rarely grow beyond fifteen members due to increasing intra-pack aggression.

As was discussed by Mech (1999), the unrelated nature of captive individuals might explain the high aggression levels found in Mission:Wolf's packs. Another related possibility that may cause increased intra-specific aggression and dominance displays in captive packs is increased competition between individuals in the pack for food, sexual partners and rank due to closeness in age.

Considering the small sample size for the number of wolves or hybrids in a pack, continued research into this factor could be beneficial. As more captive packs are observed, a clear relationship may emerge, indicating a threshold in the number of animals in a pack to reasonably minimize the risk of excessive aggression. Also, more research into the role pack size plays in wild wolf aggression would be valuable. The Druid Peak pack consisted of 26 wolves during observation, a number much higher than a typical wild wolf pack. It is possible that a smaller or larger wild pack would have different rates of aggressive behaviors. A comparison between the importance of pack size in wild and captive animals could shed more light on the reason for the specific threshold in captivity.

Applications

It may be possible to apply these findings, and future findings, to several different fields related to wolf ethology. Refuges and zoos could put to use a guideline for the number of wolves and area needed per wolf in

enclosure design for the future. At the moment, it appears they need to place their limited resources into building more, separate enclosures to facilitate smaller packs, rather than into enlarging present pens when considering the aggression level of resident wolves. Once a threshold for excessive aggression is found, such facilities could optimize the utility of their resources and increase the health and safety of both wolves and caretakers.

Another field that could benefit from observations of this trend is conservation biology. Wolf reintroduction efforts are often more successful when a 'soft release' method is used to introduce the animals to their new surroundings. A soft release is when animals to be reintroduced are kept in an enclosure at the release site for an extended period of time (Fritts 1995; USFWS 1994). The time spent in the enclosure allows the animals time to bond with each other and acclimate to the surrounding environment (Fritts 1993). The correlation between the number of wolves and aggression levels suggest that the fewer founding wolves housed together during the acclimation period, the lower the aggression level, and thus the stress level. With a lower aggression and stress level, the translocated wolves stand a better chance of forming strong bonds with each other and becoming a viable wild wolf pack once released.

Such knowledge can also be put to use in captive breeding programs for the Mexican gray wolf and the red wolf, both of which are extremely endangered. If a threshold is found for minimizing aggression, breeding and

survival success could be increased. Likewise, other ethologists and facilities around the world may be able to generalize this trend to other social pack animals that institute a strict hierarchy such as: golden jackals, Ethiopian wolves, dingoes, African wild dogs, and mongoose (Morell 1996).

Future Directions

The significance of the relationship between pack size and aggression level points toward the importance of other social factors in a wolf pack. In order to fully address the cause of heightened intra-specific aggression in captive packs, the complexity of the relationships between individuals within the pack need to be examined.

Methods similar to those used in this study could be used to look at the correlation between aggression frequencies and relatedness, stability of the pack over time, average age and variation in age within a pack. It would follow from hypotheses based upon natural selection that packs made up of more related individuals would be less inclined to be aggressive. The stability of the pack measures the amount of time the wolves and hybrids have had to establish their hierarchy. Aggression may be used at a lower frequency when reinforcing a social order that is already established. The same kind of relationship exists for the variation in age of the individuals in the pack. If the wolves and hybrids are close in age, then they will mature through the different developmental stages of their lives together. However,

if one is much older than another, they will be in conflict as each moves from one stage to another (Fentress 1967; McLeod 1997). Finally, as wolves and hybrids age, more and more of their energy is necessary to overcome the hindrance of arthritis and cancer (White 2001). Therefore, I suspect that packs made up of older individuals would have a lower frequency of aggression.

Another avenue of research might be into the effects of competition on aggression. Many refuges depend upon an unreliable food source for their animals, thus the frequency and amount of food distributed can vary greatly. In theory, if competition for food is a factor in aggression, the lower frequency and smaller quantity the feeding, the more aggressive behaviors ought to be displayed. The drive to mate and leave progeny is a basic consequence of natural selection (Bernal 1997). Competition for mates, therefore, could play a role in aggression levels. Peterson (1979) witnessed the phenomena of social rejection and aggression after subordinate wolves mated with each other or with one of the alphas. This would also be fairly simple to study in most captive situations: analyze the ratio of females to males within each pack and run a regression with aggression frequency or compare the levels of aggression in packs during the breeding season and the rest of the year. Also, refuges utilize different strategies to prevent pups from being born. By studying the aggression level of packs where individuals have been spayed, neutered, vasecotmized or are only separated during breeding season, it may

be possible to determine the effect different reproductive hormones have on aggression (Mech 1995).

Studies of different design within this area of specialization could also merit further attention. Comparing the average age at which the pack members were introduced to each other could illuminate the significance of Woolpy and Ginsberg's (1967) finding that wolf pups become less capable of forming bonds with others as they mature, with the ability virtually disappearing after seven months. In the same context of social relationships, looking into the effect domestication and hybridization has on aggression levels could be useful. It is possible that the wolves and hybrids that lived as pets in private homes during their formative years are less well adapted to the wolf social organization. Likewise, breeding wolves with dogs that have been domesticated for 10,000 years could very feasibly have an effect on a hybrid's ability to associate successfully with other wolves and hybrids (White 2001).

This study is a useful jumping-off point for much continued research into a field that has not been widely explored. The results point toward the importance of social factors rather than environmental factors in mediating aggression in captive wolves. While much is still unknown about the relationship between captivity and intra-specific aggression, the beginnings of a guideline for pack size and territory availability have been established in order to provide for increased wolf and caretaker health and safety.

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