“As the Den Turns: Pack Status as an Emergent Property of Interpack Mating Alliances and Occupation of Territory among Wolves in Yellowstone National Park, 1995-2000”

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"As the Den Turns: Pack Status as an Emergent Property of Interpack Mating Alliances and Occupation of Territory among Wolves in Yellowstone National Park, 1995-2000"

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This project represents a social scientific investigation of the emergence of patterned relations among wolf packs in a colonizing wolf population. Data analyzed were collected by the National Parks Service's Wolf Project. The formation of structurally endogamous mating alliances is explored using P-Graph methodology and Parente Suite software programs. Qualitative techniques were also employed to explore the social structure among wolf packs in Yellowstone National Park (YNP). Findings suggest that a multi-level social organization exists among YNP wolves.

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INTRODUCTION

While the emergence of social structure is of central concern to many social scientists, the general body of knowledge in this area is narrow. Some scientists have utilized simulation techniques to gain further understanding of the evolution of social networks, but empirical investigations of the emergence of structure through time and space remain a rarity. One obstacle to empirical investigation into the emergence of structure through time and space is the lack of appropriate data. Secondary, longitudinal, relational data sets containing data from an early time period, which is best for such analyses (Banks and Carley 1996), are difficult to come by. Yet another obstacle is the lack of adequate tools. At the heart of this project's inception is a secondary data set that offered a rare opportunity for this researcher to undertake the challenge of modeling the emergence of structure through time and space.

The subjects of this investigation are wolves who were translocated from Alberta, Canada and N.E. British Columbia to Yellowstone National Park in 1995 and 1996, respectively. While wolf biologists have widely documented information about intrapack relations and have depicted the wolf pack as a strict hierarchical structure, very little is known about interpack relations. This investigation, then, has two purposes: 1) to further social science knowledge of the emergence of social structure by seizing this unique opportunity to examine it from a very early stage in its formation; and 2) to generate knowledge about interpack relations among wolves. It is toward these two ends, then, that this project asks: Among wolves, is there an observable social structure beyond the pack?

LITERATURE

The Wolf

Although Mech (1970) does not consider it reasonable to attempt to compare the general intelligence of the wolf with that of other species, he reviews anecdotal evidence which he contends clearly demonstrates that the wolf shows “a high degree of adaptability to varying conditions,” (Mech 1970:9) and displays an excellent capacity for learning and retention of knowledge over long periods. Tame wolves have been able to recognize their masters after years of separation. Wolves in a particular area will learn to prey on the most abundant and easily obtainable species in that area, and will adapt their hunting habits when necessary. Trappers often relate stories of wolves learning to overcome even the most ingenious of traps (Mech 1970). In Yellowstone, wolves learned to kill Bison, which are considered among the most challenging prey for wolves, after interacting with bison for only a brief period (Smith et al, 2000).

Wolf Social Organization: The Pack

Currently, the only recognized unit of wolf social organization is the wolf pack. The most widely accepted definition for wolf pack is: “a group of individual wolves traveling, hunting, feeding, and resting together in a loose association, with bonds of attachment among all animals” (Mech 1970:8). In addition, it is widely held that the most basic element of the wolf pack is the breeding pair, the Alpha Male and Alpha Female, who are the strongest and most fit members of the pack, and who dominate and control the behaviors of other wolves within the pack. (Mech 1970; Mech et al.1998).

In his discussion of dominance within wolf packs, social anthropologist Henry Sharp (1982) calls for the employment of a sociological treatment of wolf social status. Sharp (1982) does not assume that a pack's alpha wolves earned their status through the intimidation of other packmates, nor does he further the tautological argument that the alpha is always the most fit wolf, therefore ensuring the fitness of future generations (Sharp 1982). Rather, Sharp (1982) contends that alpha status should be treated as a social position. Of alpha status, Sharp (1982) writes, "perhaps 'office' is a better term, carrying both rights and obligations, and reflective of organic solidarity (Durkheim, 1893)." Sharp, however, does not offer advice regarding the treatment of pack status, which may result from interpack relations.

Wolf Social Organization: Interpack Relations

It is held by wolf biologists that members of the pack are generally blood relatives of the breeding pair (Mech 1970; Mech et al.1998). This belief is predicated on the intense territoriality of wolves and reported observations of violent interpack hostility (Mech 1970). Non-related members of wolf packs have been observed, however, in many different wolf populations. These findings have caused considerable consternation among wolf researchers. Reflecting on the discovery of non-related wolves in several Denali wolf packs Mech et al. (1998:92) write, "The occurrence of social tolerance in a population also demonstrating widespread intraspecific strife and intolerance of strange wolves is especially puzzling."

Sharp (1982:430) contends that tolerance is necessary for the survivability of the pack: "A small group often must turn beyond its own boundaries to recruit members if it hopes to avoid extinction." It is widely known that wolves avoid mating with blood relations (Smith et al. 1997; Zimen 1982) and that most packs are family units comprised of paired adults and their offspring (Smith et al. 1997). Mating, therefore, (and thus, the survival of the species) seems contingent upon interpack relations. Moreover, an investigation of blood relatedness between packs using DNA evidence (Lehman et al. 1992) found interpack genetic similarity; "which indicates that short range dispersal […] may be a frequent occurrence" (Lehman et al. 1992:92). At the very least, then, there exists some set of interpack mating relations.

Dispersal of Individual Wolves and Pack Formation

Each instance of interpack genetic similarity represents either the union of a male and female wolf, who form a new wolf pack or alternatively, the immigration of a wolf to a pre-existing pack. Lehman et al. (1992:92) write, "a genetic connection taken alone, in concert with no other data does not differentiate" between these two types of dispersal events. Lehman et al. (1992) write that fieldwork including observations regarding eventual residences of dispersing wolves has shown that dispersers are more likely to form new packs than to join existing packs. Lehman et al. (1992) report that about twenty-five percent (25%) of the packs analyzed in the DNA study, however, represent migrations to pre-existing packs. Lehman et al. (1992:92) writes, "Such interchanges apparently occur despite the high level of aggression between wolves of neighboring packs." That the phenomenon of dispersal frequently involves the formation of new packs when wolves, whose natal packs are neighbors, pair and establish territory, and that as many as one fourth of wolf packs may include members who immigrated from other wolf packs, suggests the potential existence of a range of largely unexplored interpack relations. More generally, wolf biologists Boyd and Pletscher (1999) reviewed the current literature on dispersal reporting the existence of only ten (10) publications on the subject and also wrote that the findings on this topic were both largely inconsistent and inconclusive.

Instances of interpack migration are obvious illustrations of interpack behavior that contradict the usual assumptions of interpack hostility and aggression. The potential importance of pack formation to interpack relations, however, is less obvious; especially when it is viewed simply as an outcome of dispersal. When wolves successfully form a new pack and secure resources [namely, territory with adequate food and water] for their survival, their presence and control over these resources is tolerated, if not granted, by neighboring packs. Pack formation is of primary sociological interest for three reasons. First, the formation of a wolf pack represents a bridge between two social processes: 1) a social separation from pack members, with whom residence and resources were shared; and 2) the establishment of at least one new relationship that includes the securing of resources within the broader social context of other wolf packs and resources each has secured. Secondly, while the topic of pack formation is not directly addressed by wolf biologists, the findings of their research in areas that are most obviously related to pack formation are described by biologists as inconsistent (Boyd and Pletscher 1999) or puzzling (Mech et al.1998). It is likely that inconsistencies across studies that focus on the behaviors and social dynamics of one wolf pack at a time may represent social variability. Thirdly, the pack is the most basic and clearly definable unit of social structure among wolves and examining the formation of packs in a colonizing wolf population is the most direct route to investigating the emergence of social structure within a population of wolves.

Social Organization among other non-Humans

Much of the research on non-human social structure focuses on the formation of coalitions and alliances. Harcourt and De Waal (1992:v) define a coalition as "one-time co-operative action by at least two individuals (or units) against at least one other individual or unit," and alliances as "long-term coalitions." Coalitions and alliances are observed in the societies of many different animal taxa. These alliances and coalitions are established for a variety of reasons, including conflict intervention among macaques (Ehardt and Bernstein 1992; Silk 1992; Vasey 1996); dominance displays by spotted hyenas (Zabel 1992); cooperation in conflict between subordinate Camargue stallions (Feh 1998); and even reciprocal altruism among vampire bats (Wilkinson 1984). Moreover, scientists have examined the transfer of alliance affiliation and dominance from mother to child primates (Chapais 1992; Lee and Johnson 1992).

While the vast majority of research in this arena focuses on intra-group relations, there are a handful of exceptions in which inter-group dynamics are examined. Groups (first order-alliances) of male bottle-nosed dolphins form (second-order) alliances with other male groups for the herding and theft of female dolphins (Connor et al, 1992). Connor et al. also observed a third layer of organization, third order-alliances, but note that these interactions take the form of coalitions (temporary alliances).

Complex, hierarchical social systems are observed among Hamadryas (Sigg et al. 1982) and Gelada (Dunbar 1984;1988) baboons. Cluster analyses of association patterns among Gelada baboons reveal four levels of social organization (Dunbar 1984;1988). At the core of Gelada baboon social structure is the reproductive unit. This first level of social organization is the location for the majority of social interaction (Dunbar 1984). Bands are the second level of of organization which serve as the "basic ecological unit" of baboon society; members of the same band "share a common home range" (Dunbar 1984:17-18). Teams, an intermediate level of social organization between the reproductive unit and the band, refer to reproductive units frequently observed in close proximity to one another. It is thought that teams may be the "residual social bonds" between members of a reproductive unit that has gone through the process of fission (Dunbar 1984:17). At the fourth level are herds which represent the "unstructured consociations of units of no temporal stability" (Dunbar 1984:18).

While the existence of intrapack coalitions and alliances among wolves has been well documented (Mech 1970; Zimen, 1975; Harrington et al 1982; Pacquet et al 1982), there is no empirical work in the area of social organization beyond the pack. The incongruity between a wolf pack's occasional social acceptance of strange wolves and fierce territoriality indicates that between pack interactions may be more complex than we currently understand them to be. In light of these inconsistencies, it is illogical to conclude that our lack of knowledge regarding interpack social structure is the result of either its non-existence or some inability on the part of wolves. Moreover, there is no solid evidence to suggest that primates, for example, are more capable of generating complex social structure than other non-humans. Of the differences between primates and other animals, Harcourt (1992) writes "there is poor or even non-existent evidence that non-primates are in fact incapable of using coalitions and alliances in the way that primates do because of lack of information-processing ability." Connor et al.'s (1992) findings of second and third order alliances among bottle nosed dolphins illustrate that such complex social structure exists among non-primates.

Wolf Sociology

Sharp (1982) argues a case for the utility of a "wolf sociology" conducted by social scientists. Sharp (1982:423) contends that the lack of social science inquiry in this area has resulted in "[…] a one-sided view of animal social life that [he is] unable to justify on either theoretical or methodological grounds." Sharp writes that social scientists may be able to offer explanations about the "'whats' and 'hows' of [wolf] social life."

Sharp does not assume that there are no biological causes for behavior; rather, he contends that some social behaviors may be better explained by an examination of the social. To our knowledge of wolf social behavior, wolf sociology could contribute scientific explanations for that which we do not clearly understand.

Sharp (1982) describes three layers of wolf social organization. At the core is the domestic group, which "is not limited to reproducing animals, but is that social group 'which must remain in operation over a stretch of time long enough to rear offspring to the stages of physical and social reproductivity if a society is to maintain itself' (Forbes, 1958:2)" (Sharp 1982:429). The second layer is the corporate group, which Sharp equates to the local band within a hunting and gathering society. Of corporate groups, Sharp (1982:429) writes, "The basic corporateness of the pack does not come from continuous physical contact, but from its members' mutual support and organization for hunting and reproduction in a specific, socially bounded area." The third layer of wolf social organization described by Sharp (1982) refers to relations between packs of wolves. Sharp (1982:431) writes, "If wolf packs are involved with other packs in a geographical region, and if there is some exchange of members between packs, it is likely that this process is bounded by social factors at this higher level."

Of an investigation of the third layer of social organization of wolves, relations between packs, Sharp writes (1982:431), "Finally, if evidence is found of systematic exchange of wolves among packs, we can make a dramatic shift from recruitment to alliance theory (Lévi-Strauss, 1969) and the role of reciprocity, at which point the wolf will become a major focus of attention in the social sciences."

From a traditional social science approach, which would likely employ static, cross-sectional analyses of interpack relations, Sharp's implied prioritization of investigations represents a pragmatic and logical agenda for wolf sociology. The purpose of this investigation, however, is to gain an understanding of the emergence of social structure within a wolf society through an investigation of interpack relations. This project's most significant point of departure from Sharp's agenda lies in the question of emergence.

Kinship: Exchange and Relinking

In the study of kinship systems, the concept of exchange is fundamental. In the seminal work, The Elementary Structures of Kinship, Lévi-Strauss(1969) categorizes exchange as either restricted (direct) or generalized (indirect). Restricted exchange is a process by which there is a direct reciprocal exchange between two groups, A and B, such that if a man from group A marries a woman from Group B, the opposite must be true. Lévi-Strauss (1969:146) writes:

> The term 'restricted exchange' includes any system which effectively or functionally divides the group into a certain number of pairs of exchange units so that, for any one pair X-Y there is a reciprocal exchange relationship. In other words, where an X man marries a Y woman, a Y man must always be able to marry an X woman. The simplest form of restricted exchange is found in the division of the group into patrilineal or matrilineal exogamous moieties. (Lévi-Strauss, 1969:146)

"Sister exchange" denotes a classic example of restricted exchange and the inherent concept of reciprocity. Sister exchange is the case in which a man from Group A marries a woman from Group B and his wife's brother, in turn, marries his sister (a man from group B marries a woman from Group A). Lévi-Strauss sees such exchanges as a direct result of incest prohibition. Lévi-Strauss(1969:51) writes: "The prohibition on the sexual use of a daughter or a sister compels them to be given in marriage to another man, and at the same time it establishes a right to the daughter or sister of this other man."

Lévi-Strauss(1969) notes that many societies, however, (most notably North Australian aboriginal tribes) practice marriage systems that cannot be classified as restricted exchange. To help understand the process of reciprocity existing within these societies, Lévi-Strauss defines the concept of generalized exchange. Unlike restricted exchange, the concept of generalized exchange does not require that marriage rules be bilateral, and, therefore, the rules of exchange can be unilateral (or directional) in nature. Put another way, in generalized exchange, the fact that A man can marry B woman does not mean that B man can marry A woman. This does not imply that there is no reciprocity, but rather, that the reciprocal relationship may contain "any number of partners [moieties]" (Lévi-Strauss, 1969:178). Restricted exchange, then, represents a specific case of generalized exchange, one where the marriage rules are all bilateral, and the number of moieties involved is (necessarily) a multiple of two.

Figure 1 is an illustration of the concept of generalized exchange. The directed lines represent the allowed marriages within the system, with the arrow being drawn from the moiety of the man to the moiety of the woman. Hence, A men may marry B women (but B men may not marry A women), B men may marry C women, C men may marry D women, and D men may marry A women. There is an obvious flow of reciprocity that allows all men to have a group they are allowed to marry, although the system is more complex and less direct than that of restricted exchange.

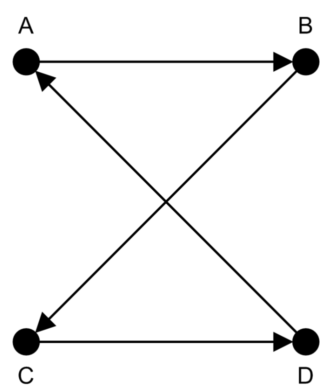

Figure 1: Generalized Exchange

Building on Lévi-Strauss' concept of generalized exchange, French structural anthropologists such as Bordieu, La Maison, and Segalen began to develop the concept of relinking (Brudner & White, 1997). Relinking occurs when, through time, the practice of a system of reciprocity causes families to intermarry over and over again. Consider the illustration of generalized exchange in Figure 1. As the cycle of reciprocal marriages (A to B, B to C, C to

D, and D to A) are repeated through time, families already linked by one marriage become relinked again and again.

Segalen(1991), when defining the concept of relinking, does not presuppose a particular sex is being exchanged, or that there is a formal exchange system (such as a bridewealth) associated with such exchanges. What is important in the concept of relinking is that there is a system of reciprocity such that a group that gives up a spouse can expect to receive one in return. Segalen (1991:122) writes:

> Within themselves, kindreds organised an active policy of exchange that was not without a certain spirit of reciprocity. If it was the logic of the struggle against dissipation of the inheritance that led to this marriage policy, each couple that had surrendered a spouse would expect to receive one, be it after a delay, be it through the medium of other couples in such a way that the patrimony did not become detached from the set of lines with which it was associated. Never mind whether the spouse was male or female. Never mind that the fact that that patrimony circulated physically without being tied to any one farm. Reciprocity must be observed for a time.

Doug White further refines the concept of relinking by introducing the concept of structural endogamy. White's (1999) argument is that all marriages are endogamous to the extent that for two individuals to enter a marriage contract, it is necessary for them to have been previously linked in some other social context perhaps as schoolmates, neighbors, or relatives. Also central to White's (1999) argument is that social status is an emergent property of kinship (White 1997; Brudner and White 1997; White 1999). A structurally endogamous kinship network is one in which marriages relink individuals previously linked by marriage. White further reasons that those with whom we share these types of pre-existent links tend be those with whom we also share status.

The use of status in this project refers to a location within a set of relations and does not imply rank. The term status group is used interchangeably with social position. Social status is defined as it is by White et al (unpublished:3):

> In the sociological tradition established by Weber […] the objective definitions of class and status are distinguished from their subjective manifestations whereby social class, for example, is a matter of the perceptions and rankings internal to a community. The approach taken here is to consider that social class may also reflect objective behavior, not as the attributes judged by outsiders, but by actions taken and relations formed by insiders relative to other insiders.

Empirically, "social class and status groups have a network component that reflects behaviors that not only link members of the group, but that relink core members to achieve redundant connectivities." (White unpublished:3) In this analysis of wolf social structure, then, pack status emerges from the relations formed through the wolves' mate selection rather than from a set of predetermined pack attributes.

White (1999) addresses the relationship between social status and structural endogamy from a complexity perspective. In simplest terms, this means that White does not posit a linear, causal relationship between these two variables. By expressing social status as an emergent property of structural endogamy, then, White (1999) posits that social status represents the 'cumulative outcomes' of marriage partner selection. By cumulative White (1999) means: 1) that social status is an emergent property of (more than one) marriage choices through time; and 2) that each marriage choice will have some bearing on the next.

In the case of this project, it makes little sense to discuss mated pairs of wolves as having entered into a marriage contract in the same way that we use this concept to discuss human kinship. It may, however, prove rather fruitful to consider that relinkages among mated pairs of wolves may represent alliances, and that formation of mating alliances may give rise to social positions among packs within a larger wolf society. Put another way, social positions among packs may be an emergent structure in the form of interpack mating alliances.

METHODS

Working Hypothesis

It should be clear that this is not an investigation of the linear relationships between social variables. In this project, social status is treated as an outcome of the relationship between mate selection and occupation of territory; where occupation of territory represents the cumulative outcomes of mate selection. At a general level, the question most central to this research is: Among wolves, is there an observable social structure beyond the pack?

In order to address the research question, the following two-part grand hypothesis was formulated:

Part I: There is a relationship between mate selection among wolves and occupation of territory by wolves; occupation of territory represents the cumulative outcomes of mate selection. Put another way, mate selection is the mechanism by which wolves have organized themselves through time and space in YNP.

Part II: The nature of social relations among packs of wolves represents a structure that may be observed as an outcome of variable mate selection and occupation of territory.

Data Description

The data used in these analyses were generated by the research efforts of The Wolf Project in Yellowstone National Park (YNP). These data were meticulously complied and coded from the National Park Service's (NPS's) Annual Wolf Reports (1995-2000), Ralph Maughan's (1995-2001) on-line Wolf Report, Nathan Varley's (2001) Wolftracker website, the Total Yellowstone Wolf website (1995-2002), Halfpenny and Thompson (1996), and Phillips and Smith (1996). The majority of the data were compiled from Ralph Maughan's (1995-2001) on-line Wolf Report and the other sources were mostly used to verify information found in Maughan's (1995-2001) Wolf Report.

In January of 1995, fourteen (14) wolves in Alberta Canada were captured and translocated to YNP. The wolves were divided into three (3) 'packs' and each pack was placed in a strategically located acclimation pen for about three (3) months. In January 1996, seventeen (17) more wolves were captured in North East British Columbia and translocated, divided into four (4) packs and also penned for three (3) months until released in YNP. The process of penning the wolves for several months prior to release is called "soft release" and its goal is to facilitate acclimation of the wolves to their new surroundings and deter them from heading north to their original homes. Later in 1996, ten (10) wolf pups of the Sawtooth Pack from another colonizing population of wolves are translocated to YNP after their parents are put to death for attacking livestock. In hopes that they would be adopted by adult wolves, the Sawtooth pups were placed in a pen with members of one of YNP's translocated packs. By the year 2000, the population of forty-one (41) translocated wolves, living in seven (7) packs, naturally grew and expanded to one hundred, eighty-nine (189) wolves living in twenty-three (23) packs.

Yellowstone National Park

A wide variety of prey exists in the Greater Yellowstone Area (GYA), including "120,000 elk, 87,000 mule deer (odocoileus hemionus), an unknown but low number of white-tailed deer, 5,800 moose, 3,900 bighorn sheep (Ovis Canadensis), 2,000 – 4,000 bison, 800 – 1,000 mountain goats (Oreamnus americanus), and 400 pronghorn (Antilocapra americanus)" (Smith, et al. 2000:1129). Since wolf packs usually consist of less than eight (8) members (Mech, 1970), the conditions of surplus may have contributed to the larger sizes among some of the YNP wolf packs. Additionally, it is reasonable to expect that surplus conditions may reduce territoriality and thus, the frequency and intensity of interpack aggression.

Generally, stability of territory held by wolf packs is relatively low (Mech et al. 1998). Mech et al. (1998:77) notes that exceptions are situations where topographical features, such as lakes or highways, might restrict wolves' movements. In addition, Mech et al. (1998) considers prey density to be a considerable factor determining stability of territory. When comparing the wolves of Denali to those he studied in Minnesota, Mech emphasizes: "the frequency of disruptive dynamics appears higher in Denali, probably because of the lower prey density there and the greater movement of the prey" (Mech et al. 1998:78). The combination of surplus conditions and topographical features of Yellowstone National Park (geysers, rivers and lakes, mountains, and highways) have likely attributed to the reasonably high stability of territory of wolves in YNP.

Constructing the Data Set

When data compilation for this project began, Ralph Maughan's (1995-2001) Wolf Report was organized as a series of narratives about each pack. Since the focus of this project is interpack relations, a single chronological narrative that would permit analyses of events occurring in and between all packs through time was much more useful. The construction of this narrative proved to be this project's most arduous task. The Wolf Report was not constructed as a data source for researchers, but rather as a vehicle for public education. Since the Wolf Report is neither a scientific data set nor a formal research report, specific bits of information about each pack, for example, were not consistently reported through time. Maughan (1995-2001) reports what he knows, most of which represents observations made by the Wolf Project and occasionally, information he receives from YNP wolf enthusiasts that he attempts to verify.

Although the Wolf Report contains a tremendous amount of in-depth information, it is not consistent and accurate enough to be used as a single source for research data. Data from the Wolf Report were first chronologically ordered and then, integrated and cross-checked with information from the other aforementioned sources. The result is a seventy (70) plus page chronology of YNP wolf related events. (An excerpt from the wolf narrative is provided in Appendix A.)

During this process it became obvious that 2000 was the last year of data collection from which any data could be considered viable for social science analyses. After this time, YNP researchers ceased their efforts to track all wolves residing in the YNP area; all wolves are no longer numbered and too few are radio collared. After 2000, the data become far too sketchy and lack the consistency necessary to be included in the analyses. In addition, after the third year or so after the restoration effort began, the information concerning the whereabouts and activities of individual, non-breeding pack members also became less consistent. It was determined, then, that the best conclusions to be drawn would be those generated from analyses of the mating-related data.

This project makes use of two types of data: 1) kinship data; and 2) interpack events data. The kinship data, consisting of wolf pairs and their offspring, are relational data that are used in conjunction with P-Graph methods (described later in this section) to model the mating structure. In contrast, interpack relational events data, although relational in nature, do not represent relations among entities; therefore, these data are not used to model social structure. These data, rather, provide, for analytic purposes, a social context in which the mating structure exists. Analyses of these events generate an enhanced understanding of the emergence of the mating structure and its relevance.

Kinship Data

After constructing the wolf narrative, information regarding wolf pairings was extracted to construct the data set. Two wolves are considered pairs when it was reported that: (1) the wolves are or are "believed to be" mates; (2) wolf 'xM' "paired with" wolf 'yF'; (3) the wolves were "observed in a [physical, sexual] tie;" (4) two wolves were observed exhibiting behaviors associated with mated pairs such as "double scent marking;" (5) one of a pack's breeding females whelps pups and a particular male "is believed to be the pups' father;" and/or (6) there is only one adult male present within a pack who could have fathered pups born to a female in that pack during that year. Table 1 provides a list of all wolf pairs, including proxies, that appear as nodes in the analysis

Table 1: All Pairs Included in the Analysis

Pair #	Date	Territory	Male	Female	Male's Parents	Female's Parents
P1	1996	Leopold	2M	7F	P2	P7
P2	1995	Crystal	4M	5F	N/A	P5
P4	1998	Crystal	104M	5F	P48	P5
P5	Pre-YNP	Canada	920M	919F	N/A	N/A
P6	1997	Crystal	6M	5F	P2	P5
P7	Pre-YNP	Canada	902M	9F	N/A	P13
P8	2000	Rose	8M	156F	P2	P9
P9	1997	Rose	8M	18F	P2	P12
P10	1997	Rose	8M	19F	P2	P12
P11	1996	Rose	8M	9F	P2	P13
P12	1995	Rose	10M	9F	N/A	P13
P13	Pre-YNP	Canada	906M	905F	N/A	N/A
P14	2000	Beartooth	916M	9F	N/A	P13
P16	Pre-YNP	Canada	903M	14F	N/A	P20
P18	1995	Soda Butte	13M	14F	N/A	P20
P19	2000	Soda Butte	104M	14F	P48	P20
P20	Pre-YNP	Canada	912M	911F	N/A	N/A
P21	Fall 1996	Washakie	15M	26F	P16	P32
P22	1998	Sheep	165M	16F	N/A	P12
P23	1997	Sheep	34M	16F	P42	P12
P24	1997	Chief	34M	17F	P42	P12
P25	2000	Druid	21M	103F	P12	P48
P26	2000	Druid	21M	106F	P12	P48

Table 1 (Continued): All Pairs Included in the Analysis

P27	Fall 1997	Nomadic	21M	39F	P12	P49
P28	1998	Druid	21M	40F	P12	P50
P29	1998	Druid	21M	42F	P12	P50
P31	Fall 1998	Teton	133M	24F	P21	P18
P32	1996	Nez Perce	28M	27F	N/A	N/A
P33	Fall 1998	Jackson/GV	29M	129F	P32	P38
P34	Fall 1998	Jackson/GV	29M	137F	P32	P38
P35	1996	Nez Perce	29M	37F	P32	P32
P36	1997	Nez Perce	29M	48F	P32	P32
P37	1998	Nez Perce	29M	67F	P32	N/A
P38	1996	Thorofare	35M	30F	P43	P32
P40	Pre-YNP	Canada	904M	32F	N/A	N/A
P41	1997	Chief	34M	33F	P42	P40
P42	Pre-YNP	Canada	908M	907F	N/A	N/A
P43	Pre-YNP	Canada	924M	923F	N/A	N/A
P44	1996	Lonestar	35M	36F	P43	N/A
P45	1996	Druid	38M	39F	P46	P49
P46	Pre-YNP	Canada	910M	909F	N/A	N/A
P47	1997	Druid	38M	41F	P46	P50
P48	1997	Druid	38M	42F	P46	P50
P49	Pre-YNP	Canada	922M	921F	N/A	N/A
P50	Pre-YNP	Canada	901M	39F	N/A	P49
P51	1998	Sunlight	52M	41F	P11	P50
P57	1999	Noname	54M	78F	P1	P9
P58	2000	Big Sky	55M	913F	P1	N/A
P69	2000	Rose	917M	77F	N/A	P9
P89	2000	Taylor	918M	115F	N/A	P24
P93	2000	Soda Butte	120M	126F	P6	P18
P114	2000	Hellroaring	161M	151F	P9	P1
P115	2000	Gardiner	914M	152F	N/A	P1
P116	2000	Absaroka	164M	153F	P22	P9

While mating data are of primary interest to Wolf Project researchers, this project's actual data set is constructed from non-scientific reports of events. These reports lack a formal coding schematic for what precisely constitutes the pairing of two wolves. The pairs data, then, as indicated above, are constructed based on a set of informal phrases that convey that particular wolves have paired. Moreover, in some cases of paired wolves, a report suggests the possibility of some uncertainty as to whether two wolves have actually paired. This is suggested by language such as, the wolves are "believed to be" mates. Since it is impossible to estimate the degree of uncertainty, if any exists, these cases are included as paired wolves. It is, therefore, possible that potential uncertainties, among either the Wolf Project researchers or the reporting sources, may have led to errors in the data set.

Interpack Events Data

As a chronological listing of wolf events, the wolf narrative contains a variety of information made available from the sources mentioned above. To analyze interpack relational events, all narrative entries representing events involving members of separate packs were copied from the wolf narrative into a separate word processing document file and are referred to as the relational wolf narrative. For ease of analysis, these entries were condensed into simple statements. For analytic purposes, then, the following entry that appeared in both the original and the relational wolf narratives:

> June 18, 1996: "Territorial battle" at Slough Creek (Rose Creek territory) between Rose Creek Pack and the Druid Peak Pack: "The Druid Peak Pack was driven off, but another of the 1995 pups, #20M, a yearling at this time, was killed as a consequence of the fight between the packs. It seems that #20M, a too-enthusiastic yearling, pursued the fleeing, but very aggressive Druids too far by himself" (Maughan 1995-2001).

is shortened to read, "6-18- 96 #20M of R.C. is killed by Druids on R.C. territory." These brief entries provided the opportunity to view a series of several chronologically ordered interpack events at one time, while preserving the essential nature of the event, which, in this case, was that Druid Peak Pack wolves attacked Rose Creek Pack wolves, killing one of them.

In the analysis of these events, two categories of events are constructed: mating and non-mating events. Between any two entities, any number of relational events may occur in any combination including across types of (mating and non-mating) events. Relational mating events are defined as behaviors which are directly related to sexual reproduction and usually occur during the wolves' mating season. Non-mating events include all known interpack interactions that are not directly related to sexual reproduction. Table 2 provides a brief listing of events sorted by event type and category.

Table 2: Listing of Interpack Mating and Non-Mating Events by Category

Mating Events

Failed Courtship Attempts

1996 Chief Joseph male is chased and injured by Rose Creek wolves.
1998 Rose Creek female is killed on Druid territory.
1998 Thorofare male is killed by Soda Butte Pack.
1999 Soda Butte male is ignored by Rose Creek Pack.
1999 Chief Joseph male is chased away by Druids.
1999 Soda Butte male is killed by Crystal Creek Pack.
2000 Leopold male rejected by Rose Creek.

Breeding Migration

1995 Crystal Creek male, 8M, migrates to Rose Creek pairing with 9F (Replaces 10M)
1997 Rose Creek male, 21M migrates to Druid Peak Pack.
1998 Druid Peak male 104M migrates to Crystal Creek Pack.
1999 Crystal Creek male 120M migrates to Soda Butte
2000 Chief Joseph male migrates to Druids as their 2^{nd} breeding male.
2000 Leopold male migrates to Rose Creek as their 2^{nd} breeding male.

'In-Laws' via Formation of a New Pack

1996 Rose Creek Female, 7F, pairs with Crystal Creek male, 2M, to form the Leopold Pack.
1996 Soda Butte male, 15M, pairs with Nex Perce female, 36F, to form the Washakie Pack.
1996 Former Lonestar male, 35M, pairs with Nez Perce female, 30F, to form the Thorofare Pack.
1997 Chief Joseph II is formed when 16F of Rose Creek pairs with Chief Joseph 34M, but dens alone.
1997 Rose creek male pairs with Druid Peak female, forming the Sunlight Basin Pack.
1998 Washakie male, 133M, pairs with Soda Butte female, 24F, to form the Teton Pack.
1998 Two females form the Thorofare pack pair with Nez Perce male, 29M to form the Gros Ventre Pack.
1999 Rose creek female pairs with a Leopold male to form the Noname Pack near the Rose Creek territory.

Non-Mating Events

Non-breeding migration

1996 Chief Joseph male migrates to the Druid Peak pack.
1997 34M's mate, 16F, migrates from Chief Joseph to den alone in Chief Joseph II.
1999 Crystal Creek male 104M (former Druid) migrates to Soda Butte.
1999 Crystal Creek male joins the Chief Joseph Pack II/Sheep Mountain Pack.
1999 Thorofare pups migrate to Washakie pack (becomes Washakie II).
2000 Chief Joseph II/Sheep Mountain. Pack male migrates to Washakie II.

Table 2 (Continued): Listing of Interpack Mating and Non-Mating Events by Category

Fighting
1996 Druids attack Rose Creek wolves on Rose Creek territory.
1996 Druids attack Crystal Creek wolves on Crystal Creek territory.
1997 Druids invade Rose Creek killing 19F and her pups.
1999 Crystal Creek yearling males attack Druid Peak Pack
2000 Chief Joseph attacks dogs
2000 Three packs in southern YNP (Washakie/Dunoir, Teton, and Gros Ventre / Jackson Trio) attack dogs.

Observed together
1996 Druid female, 39F, is observed with pups believed to be Nez Perce female 27F's displaced pups.
1999 5F (recent disperser from Crystal Creek) observed dining with Druid Peak Pack.

Visitations to Territory
1996 Two Chief Joseph males visit the Leopold's densite while the Leopold Pack is away.

Mating events are coded into three categories: 1) failed courtship attempts; 2) breeding migrations; and 3) 'in-Laws' via Formation of a New Pack. In the failed courtship attempt, a wolf (usually male) is frequently observed on another pack's territory during or immediately prior to mating season, but is rejected by that pack. In coding these data, a wolf is considered to have been rejected by another pack in instances when the wolf narrative indicated that the approaching wolf did not obtain a mate. In these cases, the three main scenarios described were: 1) a wolf returned home after his/her presence was ignored; 2) a wolf was chased away; or 3) a wolf was attacked. The second type of mating event is the breeding migration, in which a wolf (usually male) emigrates from his pack to a pre-existing pack where he immediately becomes a breeding male. A wolf is considered to have migrated to a new a pack when it was reported that s/he: 1) is "living with" that pack; 2) is "a member of" that pack; or 3) is now that pack's "Alpha/Beta Female/Male." If it is reported that a migrating wolf is "living with" the pack, is "a member of," or that s/he has a "Beta", or non-breeding, position within the pack, the event is not considered a breeding migration, but rather a non-mating event. If, however, a migrating wolf is reported to be "living with" the new pack and it is subsequently reported that the migrant is mating, the event is coded as a breeding migration. When it is reported that an immigrant assumed an Alpha position, the event is coded as a "breeding migration." The third, and final type of mating event is the resultant in-law relation that occurs between two existing packs when a new pack is formed. When it is reported that a wolf from Pack A paired with a member from Pack B, forming Pack C, this event is coded as a relational event between Packs A and B.

While the failed courtship events are not represented in the kinship data, there is some overlap of information between the kinship data and the other two categories of mating events data (breeding migration and in-laws via formation of a new pack). Information regarding both in-law relational events (via formation of a new pack) and breeding migrations is represented in the kinship data as relations between pairs of wolves. For example, if wolf 'a' migrates from pack '1' to mate with female 'b' of pack '2', their union is represented in the data as pair 'Z'. Male wolf 'a's' parents are pair 'Y' from pack '1' and female wolf 'b's' parents are pair 'X' from pack '2'. While the kinship data set do not reflect that male 'a' migrated to pair with female 'b', they do reflect that an offspring of pair 'Y' has paired with an offspring of pair 'X'. An in-law relational event is represented in the kinship data so long as both individuals posses parental nodes (real or proxy). Even though some interpack mating events are represented in the kinship data, it is not possible to ascertain, by looking only at the kinship data, which pairings are interpack events because these data do not include information regarding pack membership. Between non-mating events data and the kinship data there is no direct overlap of information.

Non-mating events are coded into four (4) categories: 1) non-breeding migrations; 2) fights; 3) wolves observed together; and 4) visitation of another pack's territory. If it is reported that a migrating wolf is "living with" the pack, is "a member of," or that s/he has a Beta, or non-breeding, position within the pack, the event is considered a non-breeding migration. In short, all reported wolf migrations that do not meet the coding criteria for breeding migration are non-breeding migrations. Reported interpack aggression which does not meet the criteria for failed courtship attempt, is coded as fighting behavior. Acts of interpack aggression include one or more members of one pack "attacking," "injuring," or "killing" one or more members of another. The third non-mating event category, wolves observed together, includes a reported observation of an adult female wolf with the (lost) pups from another pack. The final category includes an isolated event in which several members of one pack visit the territory of another pack while its members are away from their home.

This set of relational events is by no means a complete accounting of all interpack relational events among YNP wolves between 1995 and 2000. While the Yellowstone wolves remain one of the most closely observed populations of colonizing wolves, every movement of each wolf was not recorded. Fortunately, for the purposes of this project, such a complete accounting of relational events, although interesting, is not necessary. The purpose of this project's use of relational events, which is discussed in greater detail in a subsequent section, is to provide a contextual reference for the analyses of the mating structure.

Geographic Data

The geographic locations of wolf packs were obtained from information on Ralph Maughan's (1995-2001) web site. Maughan (1995-2001) constructs maps illustrating the approximate locations and territorial ranges of specific wolf packs in the Greater Yellowstone Area (GYA). Although these data are not detailed enough to be analyzed in conjunction with that of prey species in the area, they are detailed and consistent enough to provide insights into packs' general geographic locations and these locations in relation to that of other packs through time.

P-Graph Analysis

Traditionally kinship diagrams are ego-centered, such as in a family tree, where nodes represent individuals and the arcs emanating from these nodes represent parent-child relations between the individuals. This representation, according to White & Jorion (1992:454) "[…] has an inbuilt methodological individualism in keeping with the dominant social, political, and economic theories of the Anglo-Saxon world" that is "analogous to the Ptolemaic representation of rotation about the Earth that had to be abandoned centuries ago in the face of conflicting evidence." White and Jorion (1992) offer a new perspective to the study of kinship through the development of the P-Graph. A P-Graph is a graph that emphasizes the relations between marriages rather than the relations between individuals. This approach captures "[…] the fundamental sociological fact that individuals connect their parents' mating (family of orientation) to their own (family of procreation)" (White and Jorion 1992:454).

Figure 2 provides an example of a traditional kinship diagram showing martial relinking based on the marriage form known as sister exchange, in which two men marry one another's sisters. Male m, the son of couple (a,b) of Lineage A marries female s', the daughter of couple (c,d) of Lineage B. The marriage of male m and female s' creates an affinal linkage between couples (a,b) and (c,d), and thus, Lineages A and B. The two lineages and couples (a,b) and (c,d) are then, relinked, forming a new alliance, when male m' and female s marry. The focus of a traditional kinship diagrams is the ego (individual), and therefore, the relationship between the family of orientation and the family of procreation is not emphasised.

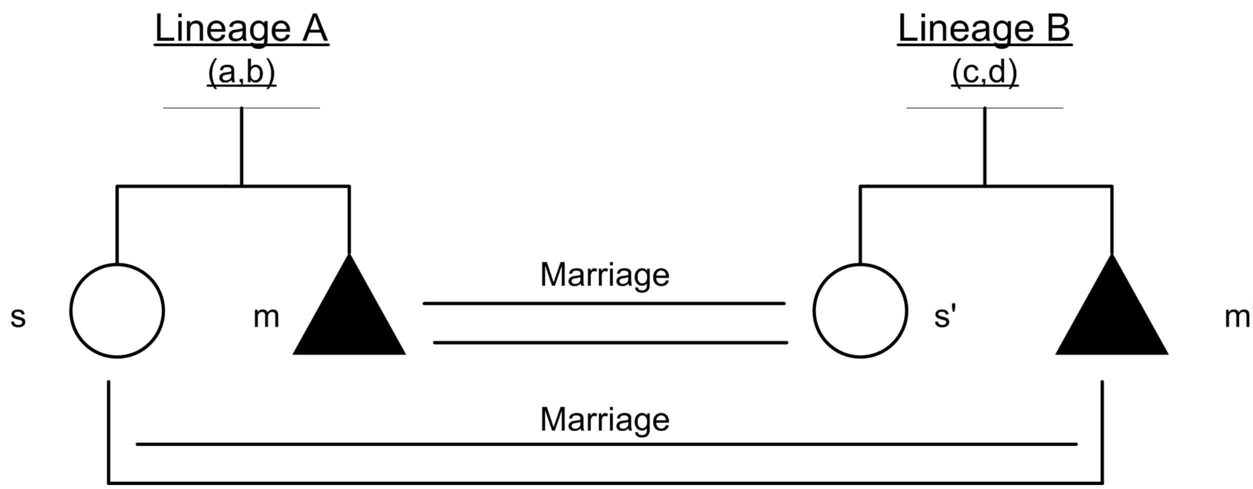

Figure 2: Sister Exchange in a Traditional Kinship Diagram

A P-Graph, however, emphasizes the relationship between families by focusing on the couple rather than the ego. Formally, a P-Graph is a signed digraph of a P-System representing a finite network of kinship with the following properties:

1. *It is asymmertric and acyclic.*
2. *The maximum indegree of nodes is 2.*
3. *For arcs of each sign the maximum indegree of nodes is 1.*

(Harary and White 2001:44).

Empirically, the P-Graph is a "finite representation of the reproductive and marital structure of a population" (White 1999:10). Nodes in a P-Graph are either personal nodes representing unmarried offspring (singletons) or marital nodes representing the marital union of two individuals of the opposite sex. The arcs drawn between the nodes are both directed (from parent to children) and signed and represent the relationship between the nodes. If a positive arc (represented by a dashed line) is drawn between two nodes, P and Q, this arc represents the relation that the members of node P are the parents of the *male* member of node Q, while a negative arc (represented by a solid line) is drawn between the two nodes would represent the relation that the members of node P are the parents of the *female* member of node Q. Since arcs are directed from parents to their children, and since no individual can have more than two parents, the maximum indegree of nodes is two (2). In addition, since the sign of the arc designates the sex of the child involved in the parent-child relation, “for arcs of each sign the maximum indegree of nodes is 1 [one]” (White, 1999:10). Since all parental data will never fall within population boundaries, the representation is always finite and, since the graph is directed and no individual can be their own ancestor, all P-Graphs are always acyclic as well (Harary and White 2001:44).

Figure 3 is an example of the kinship diagram represented in Figure 2 in P-Graph form. Instead of emphasizing the individuals, this diagram emphasizes the marriages and the relationship between the marriages, and it is abundantly clear from this diagram that each marriage (m,s') and (m',s) create a linkage between the two families (a,b) and (c,d).

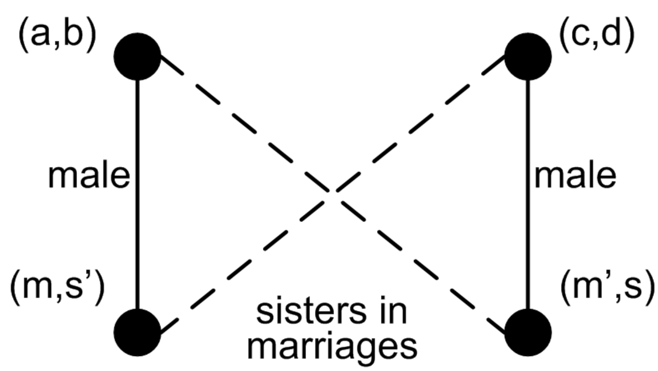

Figure 3: Sister Exchange in a P-Graph

Cycles, Blocks, and Structural Endogamy

A cycle is a path in which the starting and ending vertices are the same. If the direction of arcs in a P-Graph is ignored for the purpose of determining cycles, these cycles can be used to represent “information about marriages within and between families” (Harary and White 2001:40). A cycle in a P-Graph represents a series of “families relinking through marriage” and "is a specific realization of Lévi-Strauss's concept of generalized or indirect exchange, through a series of connected marriages" (Brudner & White 1997:164).

Formally, a block is "a maximal set of arcs and the vertices [that] they connect such that every pair of vertices are connected by a [cycle]" (White et al. unpublished:2). Hence, a block represents one or more connected cycles. Since the maximum indegree of nodes in a P-Graph is two (2), a block within a P-Graph will take the form of a bicomponent, or a subgraph that is "maximal (as large as possible)" and "every pair of nodes is connected by two (2) […] or more independent paths." Every pair of nodes in a bicomponent is "necessarily connected by a cycle" (White 1999:10).

In a P-Graph, these cycles imply a marriage that relinks marriages already linked by some prior linking, and in combination represent "a structurally endogamous block" (White 1999:10). These blocks represent a marital alliance such that every marriage in the alliance is connected by at least two paths. Therefore, the dissolution or non-existence of a single couple does not cause the dissolution of the alliance. In addition, flows of communication have two sources (Brudner & White, 1997:165).

Structural endogamy represents a special kind of endogamy, differing from ordinary or categorical endogamy, such that couples marrying individuals outside of the structurally endogamous block can still be part of the block, as long as a cycle passes through this couple to form a relinking. In this way, structural endogamy refers to a "population in which there is a tendency toward inbreeding," rather than a population that requires it (Brudner & White 1997:166). Individuals belonging to a structurally endogamous block are not restricted to marry within the block, they are merely constrained by the way their "social relationships are necessarily embedded in an emergent pattern" (Brudner & White, 1997:201).

Cycles within a P-Graph (and therefore structural endogamy) can only occur in one of two ways: through a “marriage between two persons who are related by common descent” (consanguineal, or one family relinking), or through “relinking among a sets of families who ‘marry in circles’”(affinal or multiple-family relinking) (Harary and White, 2001:42). Figure 4 shows examples of one family (consanguineal), two family (affinal, restricted exchange), and three family (affinal, generalized exchange) relinkings in P-Graph form.

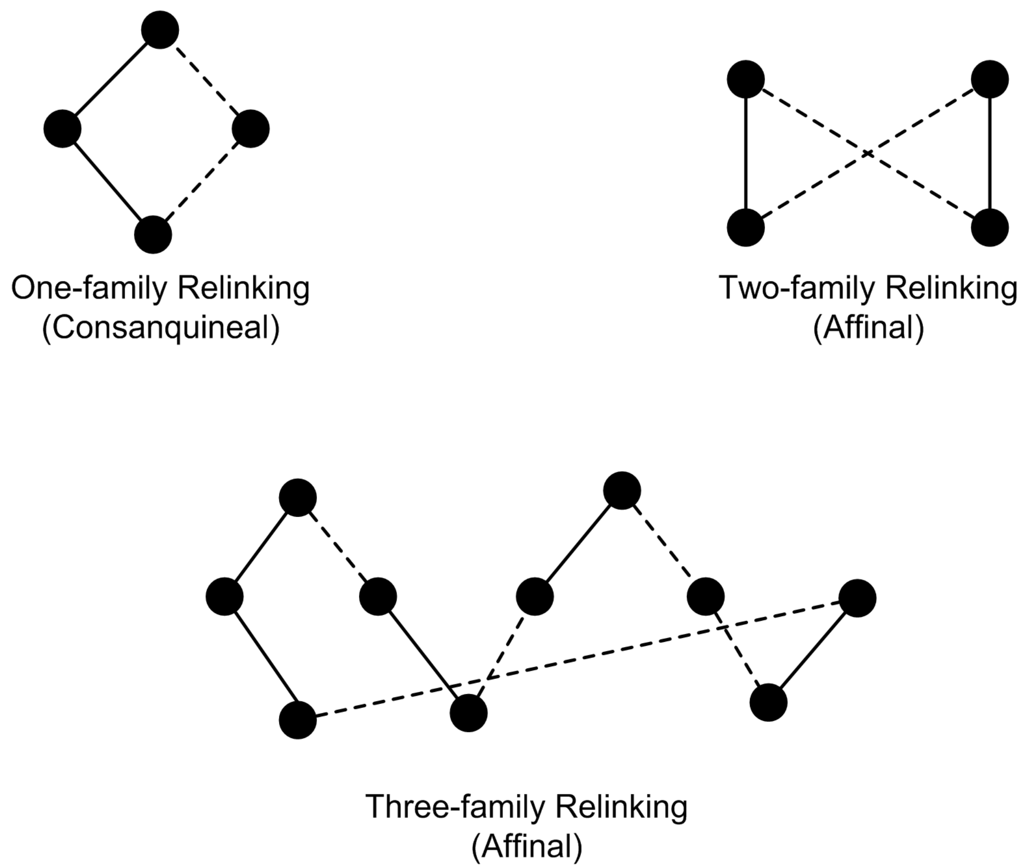

Figure 4: One-Family, Two-Family and Three-Family Relinking in P-Graph Form

Figure 5 shows the kinship diagram in Figure 2 with an additional marriage (m'',s''), that of the offspring of (m,s') and (m',s). Although it can be determined from this representation that there is some relation between this marriage and marriages in the previous generation, an exact enumeration of these relations is less than obvious.

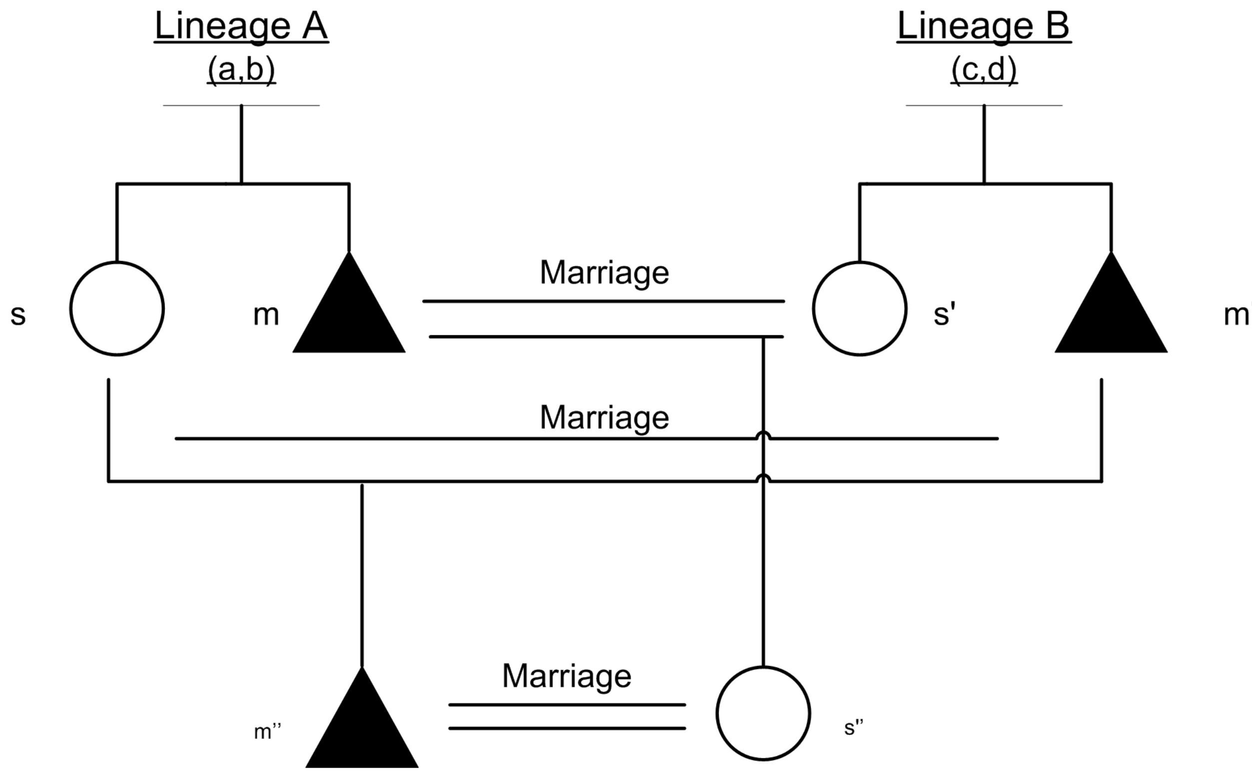

Figure 5: Cycles in a Traditional Kinship Diagram

Figure 6 is the identical marriage system from Figure 5 in P-Graph form. The cycle ((a,b) , (m,s') , (m'',s'') , (m',s) , (a,b)) tells us that this marriage represents a consanguineal union of two individuals sharing the same grandparents (a,b). In addition, the cycle ((c,d) , (m,s') , (m'', s'') , (m',s) (c,d)) tells us that this marriage also represents the consanguineal union of two individuals sharing the same grandparents (c,d). These new cycles, taken with the existing cycle of sister exchange ((a,b) , (m,s') , (c,d) , (m's) , (a,b)) create a structurally endogamous block of marriages.

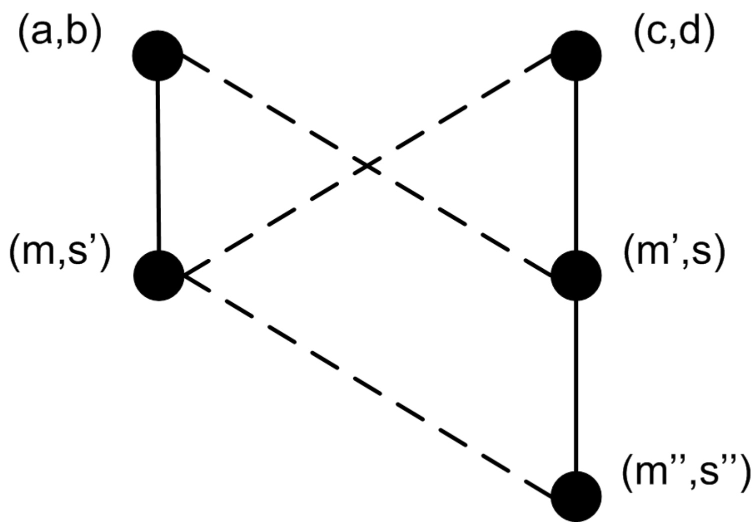

Figure 6: Cycles in a P-Graph

An interesting phenomenon resulting from the partitioning of relations based on structurally endogamous blocks is that individuals are *not necessarily* classified into mutually exclusive partitions. While it is true that the relations are partitioned into mutually exclusive sets, individuals may be multiply married. Therefore, it is possible for an individual to exist simultaneously in more than one block (Brudner & White 1997:199).

P-Graph methodology does not include a statistical test for significance of degree of connectivity within a kinship network, because it is a tool for describing sets of relations within a set of social actors. Relinking, as a type of connectivity within a P-Graph, is an attribute of the network representing a level of redundancy among relations. Redundancy ensures that a set of related pairs (a structurally endogamous block) "is not vulnerable to disconnection through removal of a single person or dissolution of a single interpersonal tie" (White et al. unpublished). As a tool, one of the most important functions of the P-Graph is that it leads to the identification of structurally endogamous blocks of relinked pairs. Redundancy in relations among relinked pairs within a given block ensures that the block is not vulnerable to dissolution. When examining relinking within a P-Graph, the question, then, is not the number of relinkings present in the graph, but rather are the present relinkings organized in such a way that they give rise to structurally endogamous blocks?

Limitations of the P-Graph

One obvious drawback of using P-Graphs is that with large data sets, the ability to clearly interpret the visual image of the P-Graph itself may be difficult. White and Schweizer (1998:38) explain that the "PGRAPH programs provide a variety of means of statistical analysis of graphs of large dimensions, regardless of their interpretability or clarity as visual images." In addition, White and Schweizer do note that the PGRAPH program, as well as many other graphical drawing algorithms available, can help to improve visual interpretation through graphical decomposition and visual structuring techniques (White & Schweizer 1998:38).

Another issue for concern applies to the observance of kinship ties in any kinship diagram, not just the P-Graph. Houseman and White (1998:66) stress that we should abandon the notion that the characteristics of a kinship diagram "automatically tell us something about the social structure," explaining that the kinship ties we uncover cannot be understood without contextual reference. Moreover, "It is not the existence of kinship ties but their activation or inactivation that is significant" (Houseman and White 1998:66).

Applications of P-Graph and Relinking Methods

In Kinship, Property Transmission, and Stratification in Javanese Villages, White and Schweizer (1998) use P-Graph methodology to study how kinship affects property flow in rural Java. By superimposing land transactions onto the P-Graph kinship diagram, White and Schweizer(1998:54) studied a kinship network where "sibling groups overlap first through intermarriage and second through the establishment of common residential blocs."(White and

Schweizer, 1998:54). For White and Schweizer (1998:55), the kinship structure creates the "scaffolding" by which "Inheritance of land, religious activities, and ensuing occupational specialization can be closely traced."

In Class, Property, and Structural Endogamy: Visualizing Networked Histories, Brudner and White (1997) use P-Graph techniques to understand how the relinking of families in a particular village within the farming valleys of southern Carinthia, Austria perpetuates a system of property transmission through social class. Within the community, transmission of class membership from generation to generation "tends to be inhomogeneous in assigning asymmetric class positions to members of the same sibling set." (Brudner and White, 1997:168). Brudner and White's (1997) main hypothesis is that the relinking of families of heired couples allowed for the creation of a structurally endogamous block of couples forming one social class, while those that married non-heir couples would not be contained within this block and would be attributed an entirely different social class, allowing for the asymmetric assignment of class positions within a sibling set. Brudner and White found that a large structurally endogamous block did exist within the community, and that this block of relations is “strongly correlated with heirship vs. nonhiership." (Brudner and White, 1997:199).

Brudner and White (1997) make a significant distinction between Lévi-Strauss' androcentric expression of generalized exchange as merely the "exchange of women." Brudner and White (1997:200) write:

> A network approach focuses even handedly on both men and women in terms of their kinship ties, inheritance, etc, and precludes choice of a "framework" of abstraction that might cast an androcentric bias of the treatment of gender roles. More basically, it allows us to take a more fine-grained approach to long-term social processes that occur in the flow of real historical time.

Parente Suite

The Parente Suite (White 1997) is a suite of programs for personal computers used to analyze kinship data based on the concepts of the P-Graph and structural endogamy. Five programs from the Parente suite were used in the analysis: Ego2Cpl, P-Graph, Par-Calc, Par-Comp and Par-Link. A description of these programs follows.

EGO2CPL

Since parent-child relationships are reciprocal in nature, the easiest way to store genealogical data is "simply to list every individual and his or her parents and [spouse(s)]" (White, et al. 1999:247). This is the most typical way in which kinship data are collected and stored. The Parente Suite program, EGO2CPL, converts from this egocentric data structure to a couple, or family-centric structure by designating family or couple numbers. During the conversion process, EGO2CPL validates the data by checking for gender discrepancies or axiomatic errors, such as being one's own parent. The program outputs files for use in other Parente Suite programs, as well as the .NET format for Pajek and the .GED format for GEDCOM.

PGRAPH

PGRAPH (White 1997) draws the "P-graph", a marriage network where nodes represent marriages (or unmarried children) and arcs represent the signed and directed relations between the nodes. PGRAPH (White 1997) also computes the number of cycles, representing structural endogamy, in the P-graph. P-Graphs generated by PGRAPH can be easily manipulated from within the program or exported for printing.

PAR-COMP

Par-Comp establishes evidence for consanguineal marriage preferences by using controlled simulation to determine if any particular marriage strategies are occurring with a greater frequency than would be expected by chance. Instead of simulating the population through time based on a series of demographic constraints, White proposes the idea of a "structurally controlled simulation." Under this approach, one gender of the parental links in the ancestral tree is held constant and for each generation, marriages are randomly permuted from the pool of individuals of the opposite gender who had married. This approach randomizes the mating regime, but holds all other characteristics of the network constant. Additional parameters may be specified to determine mating prohibitions, such as incest avoidance rules, and can be easily applied to the permutation (White 1999:13).

PAR-CALC & PAR-LINK

In Lévi-Strauss' Elementary Structures of Kinship, André Weil of the University of Chicago contributes a mathematical appendix in which he develops an algebraic notation for expressing marriage rules, based on group theory. Weil (1969:221) assumes the following:

> (A) For any individual, man, or woman, there is one and only one type of marriage which he (or she) has the right to contract
> (B) For any individual, the type of marriage which he (or she) may contract depends solely on sex and the type of marriage from which he (or she) is descended.

Weil explains that the marriage type into which a son or daughter from a marriage type M_i may contract is a function of M_i, which Weil (1969) denotes as $f(M_i)$ and $g(M_i)$, respectively, and that these functions, f and g, can be used to describe all the marriage rules within the society. For example, a marriage rule such as “a man must be able to marry his mother’s brother’s daughter” would be expressed as “$f[g(M_i)] = g[f(M_i)]$” (Weil 1969:221).

This mathematical interpretation is used as the basis for output data generated by the Parente Suite Programs, PAR-LINK and PAR-CALC. PAR-CALC focuses on consanguineal, or blood-kin relinking, whereas PAR-LINK focuses on affinal relinking. Both programs employ a shorthand for Weil’s (1969) functions of f and g, such that “fg=gf” would represent an instance of a man marrying his mother’s brother’s daughter (White & Jorion 1992:457).

BlockModeling and Regular Equivalence

Blockmodeling is most frequently used to determine structural equivalence among nodes in a network. Structural equivalence offers a foundation for understanding roles and relations in a network based on the position of nodes within that network. Figure 7 shows a simple network of parent-child relations, where C and D are the children of actor A, and E and F are the children of actor B. Actors C and D are structurally equivalent because of their common position in the network. Likewise, E and F are structurally equivalent because of their common position in the network. Actors A and B, however, are not structurally equivalent because even though both actors are parents, they are not “connected in the [exact] same way to the rest of the network.” (Doreian 1999:5). Actors are structurally equivalent only if “ the presence and absence of ties […] is the same” (Doreian, 1999:5). For actors A and B to be structurally equivalent, actor A would have to be the parent of actors E and F and that actor B would have to be the parent of actors C and D. For the same reasons pairs of actors: C and E, C and F, D and E, and D and F are not structurally equivalent. In structural equivalence, a position is formally defined as “a location in a labeled graph” (Borgatti and Everett 1992:15). Moreover, “it is about identifying *who* an actor is directly connected to” (Borgatti and Everett 1992:15-16).

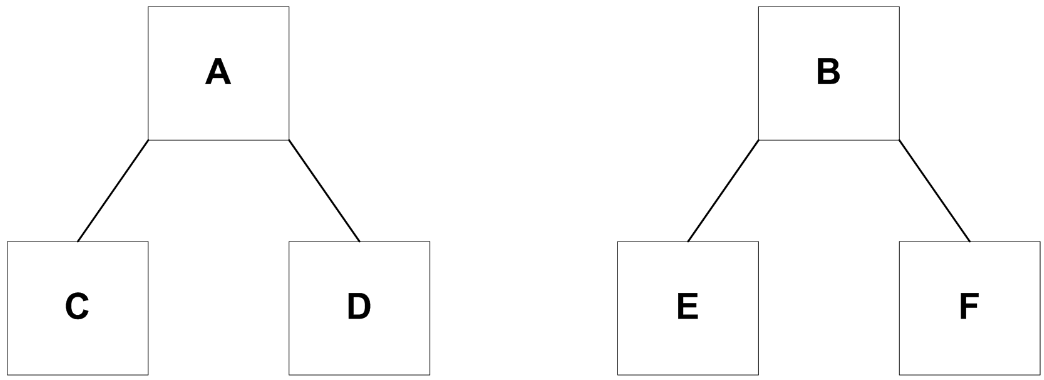

Figure 7: Network diagram representing structural and regular equivalence

The criterion for determining regular equivalence among actors in a network is less stringent. Actors are regularly equivalent if they are "equivalently connected to equivalent others" (Doreian, 1999:7). Parent nodes A and B are regularly equivalent because they are "equivalently connected to equivalent" child nodes C,D,E, and F (see Figure 7). Likewise, child nodes C, D, E, and F are regularly equivalent because they are "equivalently connected to equivalent" parent nodes A and B. In regular equivalence, position is defined as "a location in an unlabeled graph" (Borgatti and Everett 1992:16). Generally, it is "the *way* in which the node is connected to others" (Borgatti and Everett 1992:16).

Considering the matrix of ties (adjacency matrix) inherent in a network diagram, the goal of blockmodeling is the construction of an image matrix, where each "block is represented by a single element" (Doreian, 1999:14). For structural equivalence, there exists only a small number of "ideal" patterns that can form a block, and no exceptions are possible. Figure 8 represents some of the most common patterns consistent with structural equivalence.

$$\begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{bmatrix} \qquad \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$$

One Block   Null Block

$$\begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \quad \begin{bmatrix} 0 & 1 & 1 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \end{bmatrix}$$

Diagonal
Blocks

Figure 8: Patterns associated with Structural Equivalence

Regular equivalence is a generalization of structural equivalence such that blocks consistent with regular equivalence are either null (entirely filled with zeros) or 1-covered (containing at least one '1' in every row and column) (Doreian, 1999).

A further generalization, "generalized blockmodeling", provides a method for "assessing the extent to which a blockmodel is consistent with the selected form of equivalence" (Doreian, Batagelj and Ferigoj 1994:1). It allows partitions to be either column or row regular. A column regular block contains at least one '1' in every column while a row regular block contains at least one '1' in every row. In addition to allowing for different forms of equivalence, Doreian, Batagelj and Ferigoj (1994:25) write, "an appropriate generalization of the equivalence idea is one which each block, of a particular partition, is free to conform to a different equivalence idea." In addition, generalized blockmodeling provides a general criterion function that "provides an appropriate measure of fit" (Doreian, Batagelj and Ferigoj 1994:1).

Both regular equivalence and structural equivalence, unfortunately, require perfection in form that few empirical networks possess. To overcome this limitation, methods have been developed to determine blockmodels that approximate the empirical structure. These methods can be classified as either "indirect" or "direct" (Doreian, 1999). This project utilizes the direct method employed by STRAN (Batagelj 1991).

Maps

Maps are constructed to represent the distribution of packs and alliances through geographic space. Each map designates the existent wolf packs' territories at the end of the specified year. In addition, color is used to denote alliance affiliations of the Yellowstone wolf packs at the end of the year specified. A pack's alliance affiliation is designated by the shaded color of its territory with Red, Gray, Green, and Blue representing alliances 1, 2, 3, and 4, respectively. While the maps, themselves, are original productions for this project, the estimated locations of packs and groups of wolves defined as packs was obtained from information provided on Ralph Maughan's (1995-2001) web site.

Territory data will is used in conjunction with the kinship and relational events data in an effort to understand how the wolves in YNP have organized themselves through geographic space and time. More specifically, the following analyses seek to evaluate the relation between the occupied territories and interpack mating alliances; followed by an examination of the potential for the emergence of a social structure from the interplay between wolves' occupation of specific territory and the formation of mating alliances.

Sociograms

Sociograms are constructed to analyze and present relational events through time. Through the use of color, line texture, and lines directed with arrows, the sociograms differentiate among relational events on the bases of event category, quality of event, and direction (sender and recipient) of the event, respectively. The use of relational events through the construction of sociograms in this project is important for two reasons: 1) they enhance the analysis of structural endogamy by providing a contextual reference; and 2) they may be suggestive and descriptive of a potentially existent higher level of social organization beyond the measured structure. In the case of interpack relational events, relational events are used to investigate whether the structure identified in the previous analyses of the kinship data has meaning for the actors. What follows is a discussion of the construction of the sociograms.

As previously mentioned, there exists some overlap of information between the relational events and kinship data sets. Since the alliances are discovered through analyses of the kinship data, the most obvious representation of the kinship data within the analyses of relational events data are the sociograms' colors and labels illustrating which packs belong to which alliances during which years. Also of interest, however, is that some of the interpack relational events included in the sociograms are events which lead to the formation of alliances and that some of these events are included in the kinship data. Recall that there are two types of relational events: mating events and non-mating events. The overlap of information occurs between the mating events data and the kinship data. The mating events data contain three categories: 1) failed courtship attempts; 2) breeding migrations; and 3) interpack in-law relations. Only the last two categories, breeding migrations and interpack in-law relations are present in, or share content with, the kinship data that generated the alliances. Although these two categories of mating events are relational events (and are included as such in the sociograms), it is more precise to think of them as sequences of interpack events leading to the formation of alliances.

While the sociograms represent a useful way to visualize complex sets of relational events among the wolves, taken alone, the sociograms may also introduce some unintended confusion. Since each sociogram displays all of the (most recent) relational events for a year as well as alliance membership at the end of each year, interpack events that happen prior to a pack's belonging to an alliance, during the year that it allies, will appear the same as events that occurred after that pack became allied. This potential for confusion exists only during the year in which a pack allies. To alert the reader to these situations, nodes for packs allying in a given year are shaded bright yellow in that year's interpack sociogram.

Summary

In summary, this project employs a series of analytic techniques. First, the mating structure, as it evolved from 1995 to 2000, is modeled using a series of programs (EGO2CPL, P-GRAPH, PAR-CALC, PAR-COMP and PAR-LINK) contained in White's (1997) Parente Suite. , which generates output relational data for input into the other Parente suite programs. The Parente Suite (White 1997) programs are used to study the consanguineal and affinal relationships among paired wolves. The output from Parente Suite's (White 1997) EGO2CPL, which consists of all known wolf pairs and their relations, is then put into STRAN (Batagelj 1991) which is used to fit two (column) regular equivalence models: one for male ties and one for female ties. Next, relational events data are analyzed and presented as a contextual reference for the mating structure. In addition, maps are used, when appropriate to locate both the relational structure and events in geographic space of the Greater Yellowstone Area (GYA).

FINDINGS

Proxies

Proxy pairs are constructed and included in the analysis to retain to relations that would otherwise be lost. To distinguish them from other wolves, proxy wolves are assigned numbers in the nine hundreds (900's). For example, among the wolves released as the Rose Creek Pack are 9F and a daughter, 7F, that she gave birth to in Canada before being translocated to YNP. 9F's mate (who is also the father of 7F) was not captured, but the relation between 9F and 7F is retained through the construction of proxy wolf 902, who along with 9F comprise node P7. Note that it is purely coincidental that the node representing wolf 7F's parents (P7) is also named "seven" (7). Some proxy pairs are comprised of two proxy wolves and are easily recognized in Table 3 as the pairs in which both the male and female are assigned numbers in the nine hundreds (900's), such as P5 in the first row of Table 3. All seven (7) of these cases represent the construction of proxy parents for an individual who 'pairs' multiple times.

Table 3: Proxy Pairs (Wolf Pairings Comprised of One or Two Proxy Wolves)

Pair #	Date	Territory	Male	Female	Male's Parents	Female's Parents
P5	Pre-YNP	Canada	920M	919F	N/A	N/A
P7	Pre-YNP	Canada	902M	9F	N/A	P13
P13	Pre-YNP	Canada	906M	905F	N/A	N/A
P14	2000	Beartooth	916M	9F	N/A	P13
P16	Pre-YNP	Canada	903M	14F	N/A	P20
P20	Pre-YNP	Canada	912M	911F	N/A	N/A
P40	Pre-YNP	Canada	904M	32F	N/A	N/A
P42	Pre-YNP	Canada	908M	907F	N/A	N/A
P43	Pre-YNP	Canada	924M	923F	N/A	N/A
P46	Pre-YNP	Canada	910M	909F	N/A	N/A
P49	Pre-YNP	Canada	922M	921F	N/A	N/A
P50	Pre-YNP	Canada	901M	39F	N/A	P49
P58	2000	Big Sky	55M	913F	P1	N/A
P69	2000	Rose	917M	77F	N/A	P9
P89	2000	Taylor	918M	115F	N/A	P24

While preparing the data for the first Parente Suite program, Ego2Cpl, it was necessary to make some adjustments. In eighteen percent (18%), six (6) of the thirty-three (33), litters born in YNP during the study period, maternity could not be established with absolute certainty. These are situations in which two litters are born to two females living in the same pack. In some cases, the two females whelp pups in the same den. Each of the nineteen (19) wolf pups, born in these six litters, was randomly designated the son or daughter of one of the two female wolves who had whelped pups. These pups represent about twelve percent (12.4%) of the wolves born in YNP from the spring of 1995 through the spring of 1999 and ten percent (10%) of the 189 wolves in the study population.

To eliminate the possibility of systematic bias, motherhood between the two potential mothers was decided using a coin toss such that the probabilities that either of the breeding females would be designated as the mother were equal (.5). Since both potential mothers of the nineteen (19) wolf pups live within the same pack, interpack relations should remain unaffected by this decision. Of these nineteen (19) pups for whom motherhood is unknown, twelve (12) never pair as adults; one (1) dies before reaching one (1) year of age; three (3) are females who, in adulthood, join their natal pack's harem; and three (3) pair with wolves outside of their natal packs. These three wolves are 104M of the Druid Peak Pack, 153F and 161M of the Rose Creek Pack. Neither of 104M's two pairings (P4 and P19) are involved in any relinkings. Both of the Rose Creek wolves, 153F and 161M, pair separately (and each only once) as P116 and P114, respectively. Since it is unknown whether these pups were born to Rose Creek 9F or to her daughter 18F, motherhood was assigned based on the toss of a coin. It just happens that both pups were assigned to 18F's (1998) litter. During February 1998, 8M mated with both 18F and 9F to form P9 and P11, respectively. Their offspring, 153F and 161M, who pair separately to form P116 and P114, respectively, are involved in several relinkings. Since the analysis shows that these represent interpack relinkings, the formation of alliances (structurally endogamous blocks), were re-examined. This procedure involved changing one of P116's and P114's parental nodes from P9 to P11 and then, evaluating the effects on pairs' memberships in this structurally endogamous block. There is no difference in the pair composition of this block and thus, in the pair composition of this alliance (Alliance 1).

After 1999, Wolf Project research no longer kept track of every single wolf born in YNP and not all wolf pups are assigned numbers. Although the study period for this project runs through the end of 2000, even those pups born in 1999 would not be mature enough at ten months of age for the study period's last mating season in February 2000; thus, this lack of information poses no threat to the validity of the project's findings.

Relinking

Figure 9 is a re-drawing of the P-Graph that was originally drawn by PGRAPH (White 1997) using Microsoft Visio 2000. During the study period, 1995 through 2000, there are forty-three (43) pairings in total. The P-graph in Figure 9, however, displays relations between fifty-four nodes (pairings), because these data contain eleven (11) additional proxy pairs that were generated to represent pairings that occurred prior to the beginning study period. PGRAPH

(White 1997) allows the input of proxy pairs to demonstrate known relations between actors that

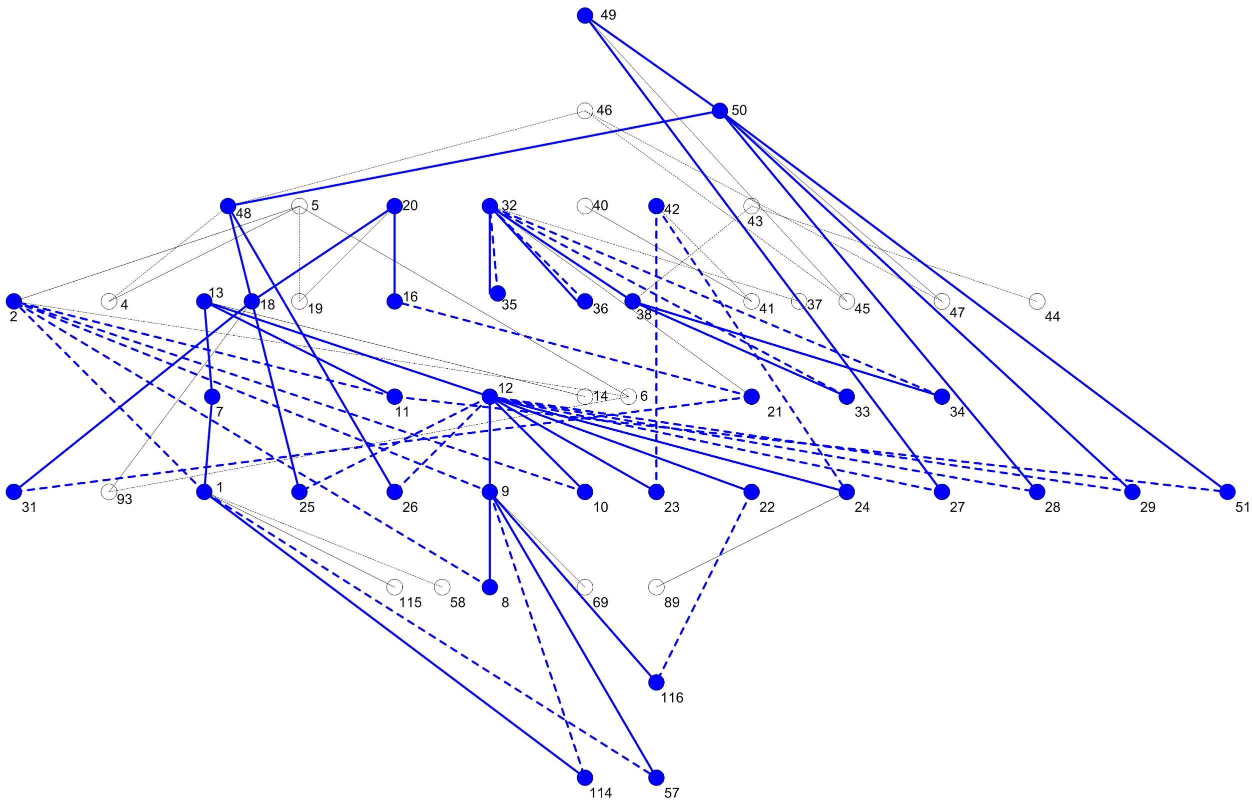

Figure 9: P-Graph Showing Relinked Mated Pairs
Blue indicates relinking among wolf pairs.

would otherwise be lost due to other missing kinship data. For example, proxy pairs were constructed for parents of siblings who were translocated, and in cases where a female wolf and her offspring were translocated, but her mate was not, data representing her relation to her offspring and the sibling relations among the pups was retained by constructing a node representing the pairing between her and an unknown wolf. The arcs between the nodes represent the relations between pairs (such as the male wolf in Pair Q is the offspring of the wolves in Pair P). Additionally, the pairs are ordered by generation with the oldest generation of wolves at the top of the graph and the youngest generation at the bottom.

As previously stated, the P-Graph is a kinship diagram emphasizing mating relations. Consider the nodes P1 and P10 in Figure 9. These nodes represent the pairing of wolves 2M and 7F and 8M and 19F, respectively. The dashed arcs descending from P2 into both P1 and P10 show that both matings involve the male offspring of P2 (4M and 5F); hence 2M and 8M are brothers.

It can also be easily determined from the P-Graph that the female wolves in this pairing are related as well. Tracing the solid lines emanating from nodes P1 and P10 up through the graph we find that they intersect at P13 (905M and 906F), traveling through marriages P7 (902M and 9F) and P12 (10M and 9F). P7 and P12 represent two different matings of wolf 9F. Hence, the female wolves in couple 1 (7F) and 10 (19F) are maternal half-sisters. This is called an affinal relinking, because two brothers born of couple 2 have both linked by marriage the family of couple 13, by marrying two maternal half-sisters. The pairs P1, P2, P10, P12, P13 and P7, therefore, represent a cycle. Since P9 represents another mating between a son of P2 (8M) and a daughter of P12 (18F), the cycle P2, P9, P12, P10 represents another affinal relinking. (See Appendix A for excerpts from the wolf narrative corresponding to these data.)

In Figure 9, all nodes and arcs involved in relinking have been drawn in blue. In the P-Graph (see Figure 9), relinkages are easily identified. Figure 9 shows twenty- eight (28) endogamous pairings in twenty-three (23) cycles. Nearly three quarters (74%) of pairings in which both wolves are known and numbered (38 in total) represent relinkages.[1]

Parente Suite (White 1997) analyzes two types of marital relinking in kinship systems. Par-Calc enumerates blood-kin relinkages (incest marriages) by familial relation while Par-Link generates of list of pairs of pairs relinked by affinal marriage (marriage between in-laws). The

[1] This is not reported as a measure of the degree of relinking, but only as a description of proportion of pairs involved.

Parente Suite (White 1997) programs identified both blood-kin and affinal relinking among the wolves. First, Par-Calc (White 1997) identified nine pairs, twenty-four percent (24%) of all pairs, or thirty-two percent (32%) of relinked pairs as marriages between blood relatives.

Of the twenty-eight (28) endogamous pairings, nineteen (19), or sixty-eight percent (68%), represent affinal relinkages of blood relatives. Par-link (White 1997) was used to generate a list of these pairs and the relations between them. The following is an example of an example of an expression called a P-Link from the Par-Link (White 1997) output:

7G =FG46 + 7F =G 46

This is an expression of relation between pair numbers seven (7) and forty-six (46), where G is used to represent the parents of the male in a pair and F is used to represent the parents of the female in a pair. The P-Link above, then, states that the parents of the male in pair number seven (7) are the same as the paternal grandparents of the female in pair number forty-six (46), and that the parents of the female in pair number seven (7) are the same as the parents of the male in pair number forty-six (46).

The P-Links were sorted into groups of similar expressions, or variants, and translated into verbal statements. Par-link (White 1997) output generates a P-Link for each relation between two pairs so there may be (and often are) multiple P-Links containing relational information for any two given pairs. In these instances the simplest expression or "closest" statement of relation was retained.

A peculiarity of P-graph notation is that it is impossible to differentiate between one male pairing with two related females and two brothers pairing with two related females. The basic structure for the 'male' part of the expression of either situation would be G=G. Since there are several known instances of YNP males mating with more than one female, it was necessary to manually verify the P-links to accurately differentiate between statements representing relations among four wolves and those representing harem-like relations among only three (one male and two female wolves).

The other, non-polygamous, half of the forty-six P-links are statements of affinal relinking among four wolves; or put another way, two sets of blood related wolves who become relinked as ‘in laws’ through mate selection. In seventy-four percent (74%) of these P-links, the blood relatives are of the same sex, indicating that the YNP wolves show a preference for obtaining mates via relinking the pairings of their same-sexed relatives.

Relinking is also patterned by generation and sex. In sixty-one percent (61%) of these P-links, a pairing relinks a pairing from a previous generation, such as a son’s pairing relinking his parents or a nephew relinking his aunt’s and uncle’s pairing. Thirty-nine percent (39%) represent relinking within the same generation, for example a sibling relinks a sibling’s pairing or a cousin relinks a cousin’s pairing. Blood related males were more likely to relink pairings from a different generation (58%) than from the same generation (42%). Among related females, this preference for relinking across differing generations (76%) is more pronounced.

Results pertaining to particular familial relations should be received with caution because of the aforementioned difficulty in determining maternity among females living in harems. Of course, this is a not a discussion of relinking among wolves currently living in harems, but for those wolves born into harem families, this ambiguity extends to the sibling, cousin, niece, nephew, son and daughter relations which may define affinal relations. As previously mentioned, in these ambiguous situations, motherhood of nineteen (19) harem pups was randomly assigned to females known to have denned and whelped pups in that pack during that year. These nineteen pups represent ten percent (10%) of the 189 wolves in the study population. Of the seventeen (17) pairs of wolves who affinally relink pairings of same sex-relatives, five (5) or twenty-nine percent (29.4%) have randomly assigned mothers. The following results, then, should be interpreted with some caution.

The ten related males from different generations who relink are evenly split between father-son and uncle-nephew. Same-generation relinking males, however, may favor brothers to cousins, with frequencies of six (6) and one (1), respectively. Among female relinkers, there was a slight preference for mother-daughter (61%) vs. aunt-niece (39%). In contrast to relinkings among males, female wolves may demonstrate a preference for relinking cousin relations (75%) over sibling relations (25%). Again, these figures should be interpreted with some caution.

Interestingly, twenty-one (21), or nearly half of the forty-six (46) P-links represent harem mating arrangements. The eighteen (18) harem-like pairings represent forty-two percent (42%) of the total wolf pairings in YNP from from 1995 through 2000. Seventy percent (70%) of harem-like P-links are among one male and a female plus her daughters from a previous pairing or her nieces. The other thirty percent (30%) are instances of a male with sororal wives. In six (6) of the seven (7) instances of sororal wives, the male pairs with both at the same time. Half, or three (3), of these simultaneously forming sororal harems are expansions of an existing pairing or harem between/among a male and a female from the previous generation.

Intrapack vs. Interpack Relinkings

Since the primary focus of this investigation is interpack social structure, the next step was to differentiate between intrapack and interpack relinkings. The relinkings were sorted into three categories: 1) relinkings between packs; 2) relinkings within packs; and 3) relinkings between pairs of wolves who were once members of the same pack, but are now members of different packs due to fission of the original pack (see Table 4). Of the forty-six (46) relinkings, fifty-nine percent (59%) are interpack, thirty-nine percent (39%) are intrapack, and one (1) relinking is among wolves

Table 4: Relinkings by Type

Pair 1	Pair 2	Pack 1	Pack 2	Type of Re-linking	Natal Packs of Pair 1 Wolves	Natal Packs of Pair 2 Wolves
23	24	Sheep Mtn.	Chief Joseph	FISSION		
27	51	Druid	Sunlight	INTER	(Rose/Druid)	
114	116	Hellroaring	Absaroka	INTER	(Rose/Leo)	(Sheep/Rose)
1	114	Leopold	Hellroaring	INTER	(Rose/Leo)	(Rose/Leo)
1	57	Leopold	Noname	INTER	(Rose/Crystal)	(Leo/Rose)
1	9	Leopold	Rose	INTER	(Rose/Crystal)	
1	10	Leopold	Rose	INTER	(Rose/Crystal)	
1	11	Leopold	Rose	INTER	(Rose/Crystal)	
35	33	Nez	G.V./Jack	INTER	(Thoro/Nez)	*same male
36	33	Nez	G.V./Jack	INTER	(Thoro/Nez)	*same male
35	34	Nez	G.V./Jack	INTER	(Thoro/Nez)	*same male
36	34	Nez	G.V./Jack	INTER	(Thoro/Nez)	*same male
57	116	Noname	Absaroka	INTER	(Leo/Rose)	(Sheep/Rose)
57	114	Noname	Hellroaring	INTER	(Leo/Rose)	(Rose/Leo)
57	8	Noname	Rose	INTER	(Leo/Rose)	
8	116	Rose	Absaroka	INTER		(Sheep/Rose)
9	116	Rose	Absaroka	INTER		(Sheep/Rose)
10	116	Rose	Absaroka	INTER		(Sheep/Rose)
8	114	Rose	Hellroaring	INTER		(Rose/Leo)
9	114	Rose	Hellroaring	INTER		(Rose/Leo)
10	114	Rose	Hellroaring	INTER		(Rose/Leo)
9	57	Rose	Noname	INTER		(Leo/Rose)
10	57	Rose	Noname	INTER		(Leo/Rose)
51	25	Sunlight	Druid	INTER	(Rose/Druid)	
51	26	Sunlight	Druid	INTER	(Rose/Druid)	
51	28	Sunlight	Druid	INTER	(Rose/Druid)	
51	29	Sunlight	Druid	INTER	(Rose/Druid)	
21	31	Washakie	Teton	INTER	Soda/Nez	Washakie/Nez
28	25	Druid	Druid	INTRA		
29	25	Druid	Druid	INTRA		
25	26	Druid	Druid	INTRA		
28	26	Druid	Druid	INTRA		
29	26	Druid	Druid	INTRA		
27	28	Nomadic	Druid	INTRA		
27	29	Nomadic	Druid	INTRA		
28	29	Druid	Druid	INTRA		
47	45	Druid	Druid	INTRA		
45	48	Druid	Druid	INTRA		
47	48	Druid	Druid	INTRA		

Table 4 (Continued): Relinkings by Type

33	34	G.V./Jack	G.V./Jack	INTRA
35	36	Nez	Nez	INTRA
9	8	Rose	Rose	INTRA
10	8	Rose	Rose	INTRA
11	9	Rose	Rose	INTRA
9	10	Rose	Rose	INTRA
11	10	Rose	Rose	INTRA

and one (1) relinking is among wolves who were once members of the same pack. Figure 10 provides a visual representation of the ratio of intrapack to interpack mating relations. The red nodes and arcs represent interpack relinking, while the black nodes and arcs represent those pairs not involved in interpack relinking.

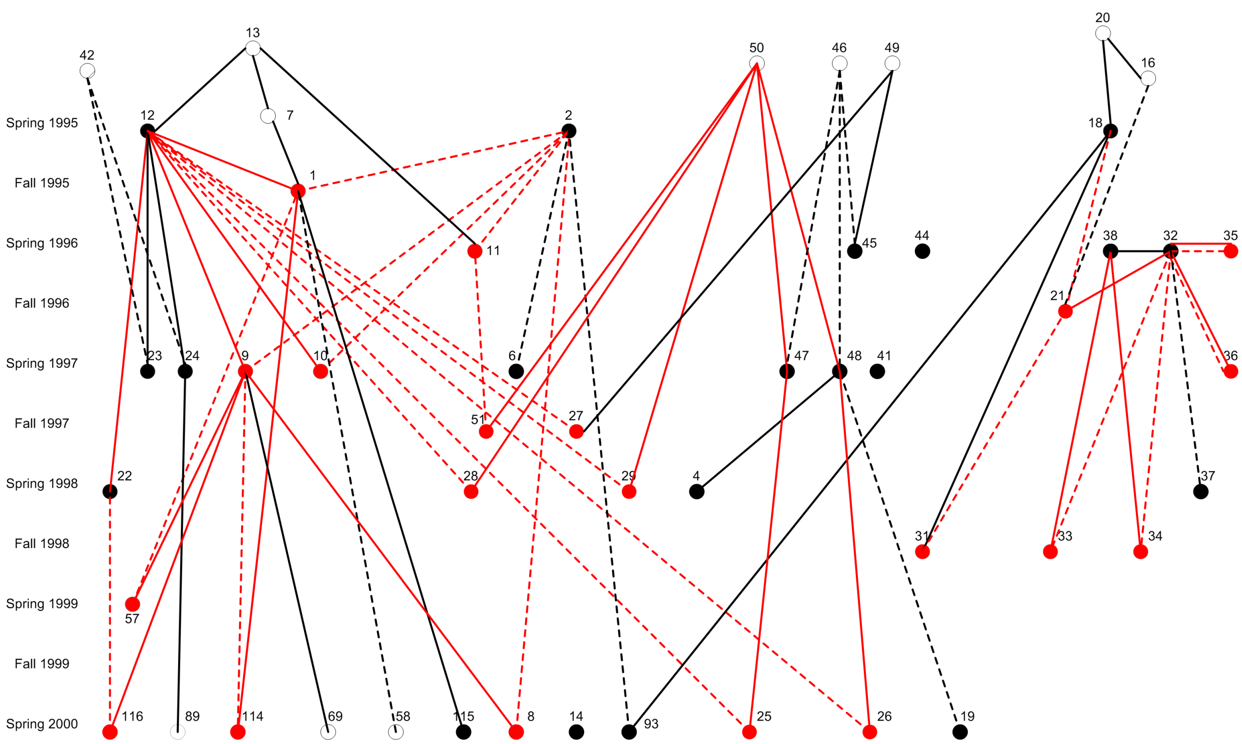

Figure 10: Intrapack vs. Interpack Mating Structure
Red denotes interpack relinking among wolf pairs. Black denotes intrapack relinking and absence of relinking among wolf pairs.

Wolf Packs: Intrapack Mating and Territory

None of the intrapack relinkings are among two separate pairs of wolves (4 individual wolves). All but two (2) are polygynous groupings of one (1) male and two (2) or more female wolves. The two exceptions are the P-links (involving P28 & P27 and P29 & P27) between the Druid Pack and the pack called "Nomadic" (see Table 4). While each of these links also only involve three (3) wolves, neither represents a reproductive unit. The male wolf (21M) in all three (3) pairs (P27, P28, and P29) dispersed from his natal pack and paired briefly with 39F, a 'lone' disperser from the Druid Peak Pack, to form P27. Shortly after the two paired, the only male members of the Druid Peak Pack were killed in two separate shooting incidents. 21M quickly moved into the Druid Peak Pack as its new breeding male, where he mated with two Druid females (forming P28 and P29), both of whom are 39F's daughters.

Generational Transmission of Territory

Figure 11 is the PGRAPH drawing with nodes colored to represent specific territories occupied by pairs and arcs colored to represent the inheritance of territory by offspring's pairing.

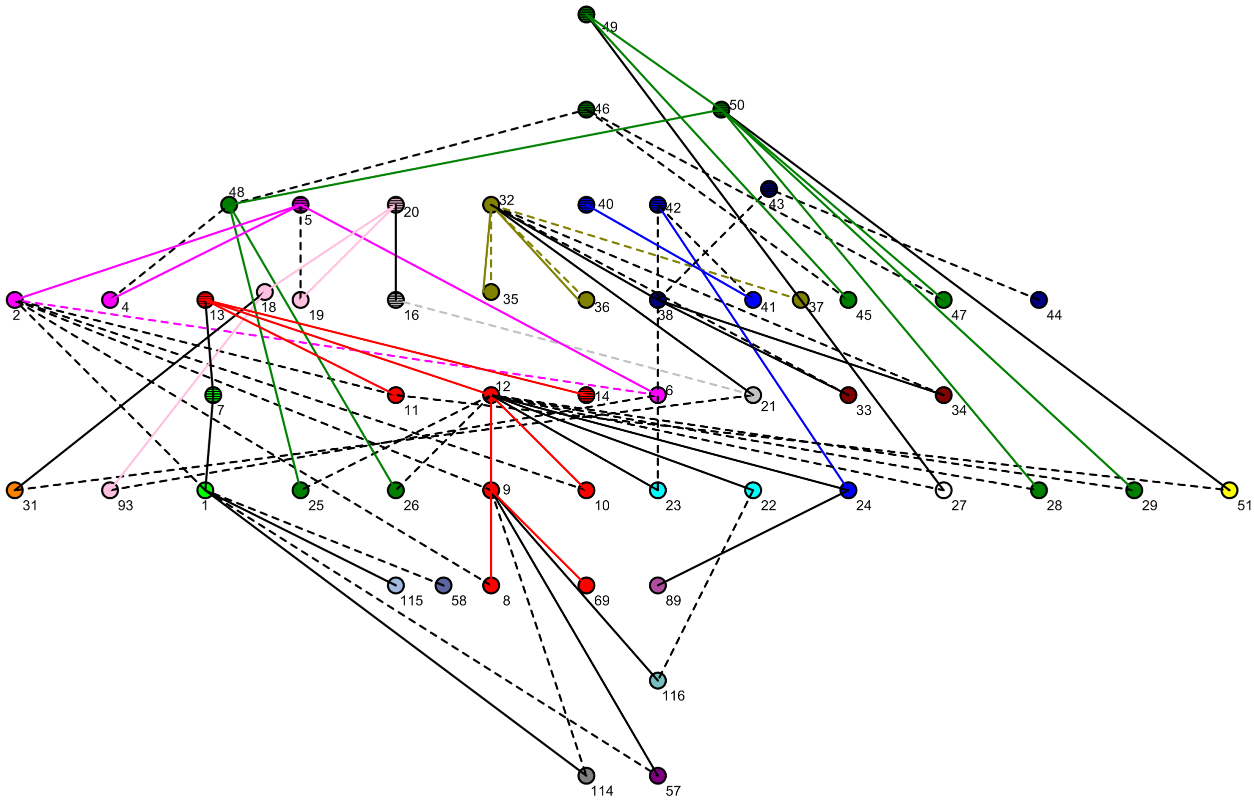

Figure 11: Flow of Territory Superimposed on P-Graph Drawing
Colors denote packs and their territories as follows: Dark green=Druid Peak Pack; Red=Rose Creek Pack; Khaki=Nez Perce Pack; Dark Pink=Crystal Creek Pack; Light Pink=Soda Butte; Dark Blue=Chief Joseph.

Figure 11 shows only three (dashed) lines with color, one dark pink from P2 to P6 and two yellow lines from P32 to P35 and P36. Interestingly, each of these three instances are blood-kin relinkings. The bright pink territory appears to be transmitted from P2 to their son and his mate, P6. This, however, is an unusual case in which a male wolf (the male in P6) pairs with his mother (the female in both P2 and P6) and they reside on the same territory, called Crystal Creek. The two yellow dashed lines traveling from P32 to P35 and P36 are both accompanied by solid yellow lines. P35 and P36 contain the same male, 29M, who pairs with two of his own sisters. Female wolves are much more likely, then, to inherit territory from their parents than are males. Moreover, females are much more likely to mate in their natal packs than are males; thirty-four percent of paired females (34%) compared to two percent (2%) of paired males. This pattern, no doubt, is related to the large proportion (42%) of wolf pairings that are actually harem arrangements. Take, for example, the transmission of Rose Creek territory through three generations of breeding females in that pack represented by the solid red line from P12 to P9 to P8. In this instance, the female in P9 (wolf 18F) who was born of P12 (9F and 10M) pairs with her stepfather (8M), who will also pair with their (8M's and 18F's) daughter (8F), forming P8. Although it may look as if P13 might represent the great grandmother of 8F in P8, P13 is actually a proxy pairing (note the horizontal black lines in its red node) that is used to show relationships between P11, P12, and P14. All three of these nodes (P11, P12, and P14) represent the pairings of 9F. As mentioned previously, P-Graph does not differentiate between siblings and the same individual involved in multiple marriages.

Central to this investigation is the relationship between the mating structure and the occupation of territory. Just as Figure 11 shows that most colored nodes contain females who have inherited territory, most also contain a male who has emigrated from his natal pack to mate. In Figure 11, the colored nodes with two black lines, one solid and the other dashed, represent the acquisition of new territory (formation of new packs). These are instances in which both males and females migrate from their natal packs in order to mate. In nine (9) of the eleven (11), or seventy-eight percent (78%), of the packs formed in which the male and female are both known are relinkings. Clearly, there exists a relationship between YNP wolves' mating structure and the occupation and acquisition of territory.

Acquisition of Territory

STRAN (Batagelj 1991) was used to fit column regular equivalence models for the mating data. Since the majority (74%) of affinal relinkings are among same-sex relatives, two models, male ties between pairs and then, female ties between pairs, seem more appropriate than one model containing all of the ties. Moreover, previous findings of the relationship between flow of territory and the mating structure suggest that the interplay between territory and mating may represent two different processes; one for males and another for females.

While prior examination of the relationship between the mating structure and territory via examination of Figure 11 seemed to provide more information about this process among female wolves than for males, the column regular equivalence model made it possible to identify a pattern among generations of males that may have otherwise been overlooked. Interestingly, a pair's method for acquisition of territory appears unrelated to female's generation. The figures, however, originally constructed in DOT (Ganser 1999), which show the column-regular partitions generated by STRAN (Batagelj 1991) are shown in Figures 12 and 13 below.

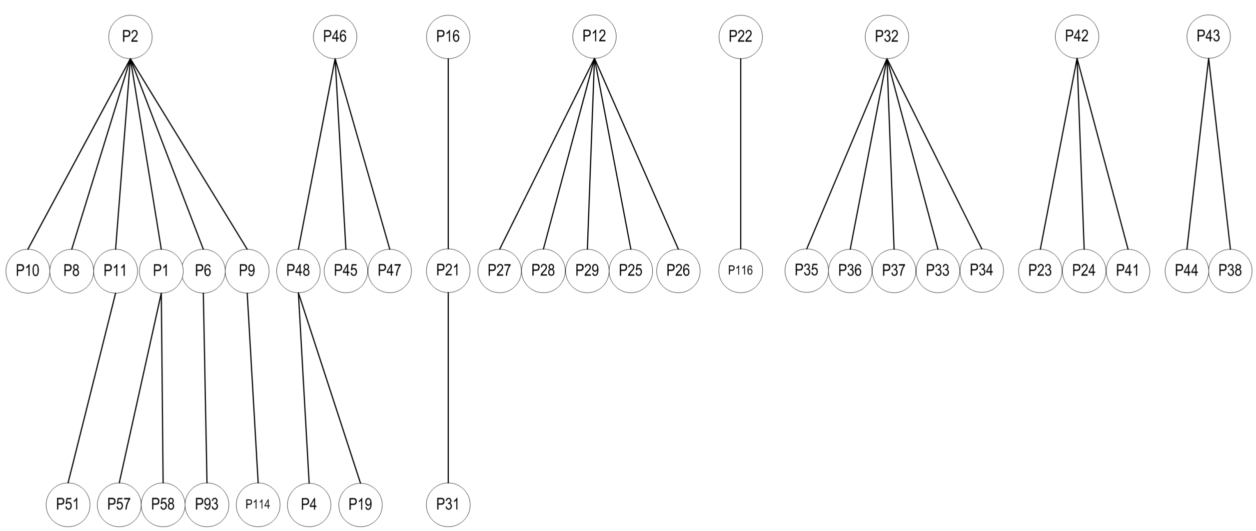

Figure 12: Column Regular Partitions (Male Ties)

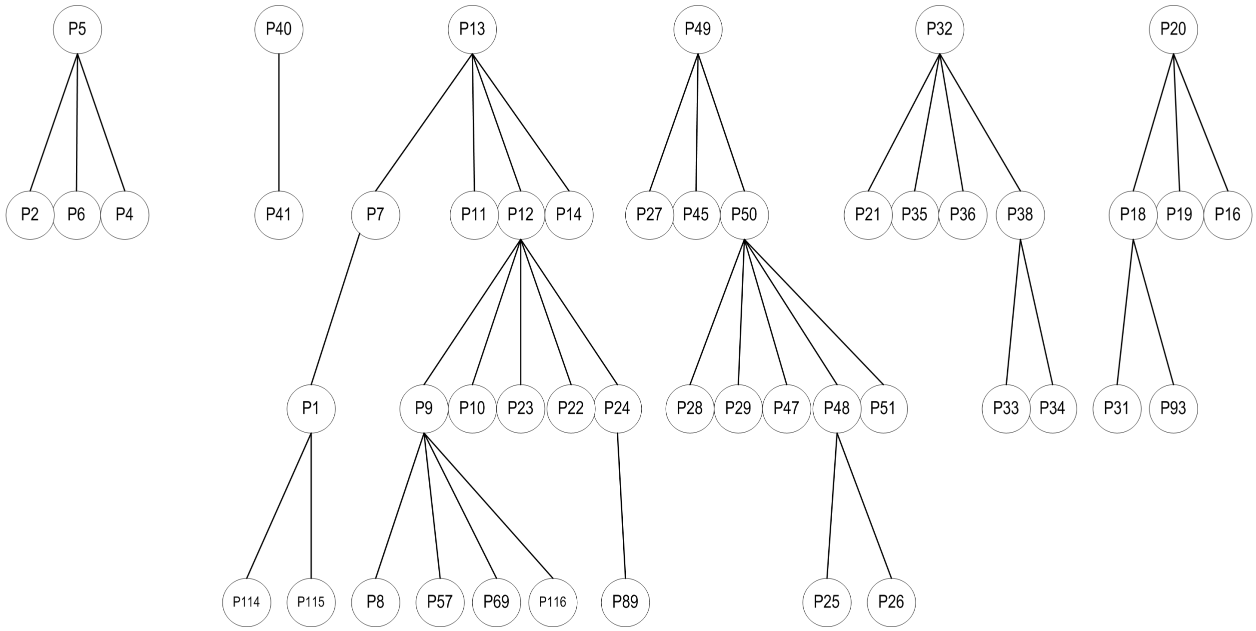

Figure 13: Column Regular Partitions (Female Ties)

Recall that Figure 11 contained both male and female ties with the occupation and generational transmission of physical territory superimposed on the network. Specifically, it was learned that territory flowed from one generation to the next via matrilines, with two exceptions in which males had paired with blood relatives and therefore were also occupants of their natal pack's territory. It was also observed that among the new packs formed in YNP in which both the male and female are known, seventy-eight percent (78%) are relinked pairings. Aside from this relationship between relinking and the migration of a male and female to new territory, this type of analysis provided little insight to the method by which territory is acquired. Since there is a relationship between mating and the occupation of territory, it makes sense to further explore the potential relationship between mating and the ways in which territory has been acquired.

If pairs of wolves occupy territory, there are four (4) ways in which those pairs have acquired their territory: 1) pairs were released on that territory during translocation to YNP; 2) a male migrates to an existing pack and pairs with one or more females on that territory; 3) a male and female (from different packs) both migrate forming a new pack on new territory; and 4) wolves pair on the territory where they reside. The distribution of pairs across these categories of methods for acquisition of occupied territory were examined in conjunction with the three (3) clusters, or generations, generated by the STRAN (Batagelj 1991) for male ties between pairs (see Table 5).

Table 5: Generational Clusters by Pack and Territory Acquisition Style

Acquisition of Territory	Cluster A	Cluster B	Cluster C
Released on Land	Crystal 1995 P2 Rose 1995 P12 Soda 1995 P18 Nez 1996 P32	Chief Joseph 1996 P41 Lonestar 1996 P44 *Druid 1996 P45*	NONE
No Land	NONE	No Pack 1997 P27	NONE
Same Land	NONE	Crystal 1997 P6 *Nez 1997 P36* *Rose 1997 P9 P10* *Druid 1997 P47 P48* *Nez 1998 P37* *Rose 2000 P8* *Druid 2000 P25 P26*	NONE

Table 5 (Continued): Generational Clusters by Pack and Territory Acquisition Style

Male Migrates	Sheep 1998 P22	*Rose 1996 P11*	Crystal 1998 P4
		Druid 1998 *P28* *P29*	Soda 2000 P19 P93
New Land	NONE	Leopold 1996 P1	Sunlight 1997 P51
		Thorofare 1996 P38	Teton 1998 P31
		Washakie 1996 P21	Noname 1999 P57
		Nez 1996 P35	Hellroaring 2000 P114
		Sheep 1997 P23	Big Sky 2000 P58
		Chief Joseph 1997 P24	
		G.V./Jackson 1998 *P33* *P34*	
		Absaroka 2000 P116	

Note: Underlined and italicized entries represent harem arrangements

The three (3) clusters represent an ordering of the pairs by the male's generation and are labeled Cluster's A through C, where Cluster A represents the oldest generation and Cluster C the youngest. Constructed as an analytic device, Table 5 also contains additional information regarding pack (territory occupied), year of pairing, and type of arrangement (harem or one male and one female). Entries representing harem arrangements are underlined and italicized in Table 5.

The most obvious pattern in Table 5 is that all of the harem arrangements are concentrated in Cluster B, the middle generation of males. These findings compliment the National Park's Service's acknowledgement of polygynous mating behavior in the Wolf Project's Annual Report for 1999. Smith et al. (2001:16) write, "Preliminary results suggested that immediately after reintroduction, Yellowstone wolves were more polygynous than in areas characterized by wolves in long standing populations." Interestingly, the association between polygynous mating and year of pairing appears moderate at best with the Rose Creek and Druid Peak Packs both expanding the size of their harems by one (1) and two (2) females, respectively, in 2000. An examination of these data by generation, such as the tools employed in this project have allowed, reveals that all polygynous behavior is isolated to this second, or middle, generation of YNP male wolves.

Also of interest is that at least the male member of each pair in Cluster C, the pairings containing the youngest generation of males, migrated in ordered to acquire territory. All of the cases of pairing on the 'same land' are Cluster B pairings. The male wolves in this category are either paired with a blood relative or are adding pairs to form or increase a harem arrangement on land they had acquired through either their own release in YNP or through a migration to pair with a female (or more than one female) on her (their) land. None of the males pairing on land they had occupied prior to mating had acquired it as new land. In addition, none of the packs that have formed in YNP are harem arrangements.

These findings, that mating form (polygamous vs. monogamous) and territory acquisition strategy are much more strongly related to generations of males than females suggests that generation may carry a greater social significance for males than it does for females. That mating form and territory acquisition are much more strongly associated with male generation than time, may suggest that, among YNP male wolves, generation may represent a social position and an associated social role in the process of the organization of wolf packs through time and space in YNP.

Wolf Mating Alliances (Interpack)

The next step in the project was to examine the P-Graph to determine the existence of mating alliances. Recalling the concept of the structurally endogamous block, the wolf pairings involved in cycles of relinking were grouped into clusters such that their aggregation would form a bicomponent within the P-Graph. Put another way, all the cycles in the P-Graph that are connected by at least two nodes form a structurally endogamous block and are considered members of the same mating alliance. Table 6 shows the pairs and packs that comprise each of the four structurally endogamous blocks, or mating alliances.

Table 6: Four Mating Alliances

Alliance 1		**Alliance 2**		**Alliance 3**		**Alliance 4**	
Pair Nos.	Pack	Pair Nos.	Pack	Pair Nos.	Pack	Pair Nos.	Pack
1	Leopold	32	Nez 1	18	Soda 1	12	Rose 1
2	Crystal 1	35 36	Nez 2	21	Washakie	23	Sheep 1
12	Rose 1	33 34	Jackson/G.V.	31	Teton	24	Chief 1
8 9 10 11	Rose 2	38	Thorofare	16 20	N/A (Proxy Pairs)	42	N/A (Proxy Pairs)
22	Sheep 2						
45 47 48	Druid 1						

Table 6 (Continued): Four Mating Alliances

25 26 28 29	Druid 2
27	Nomadic
51	Sunlight
57	Noname
114	Hellroaring
116	Absaroka
7 13 46 49 50	N/A (Proxy Pairs)

Alliance 1, the largest alliance in the park, contains mated pairs from 12 different packs in Yellowstone National Park. Alliance 2's membership stems from four (4) packs, and both Alliances 3 and 4 are comprised of wolves from three (3) packs. Note that P12 is located in both Alliances 1 and 4. As structurally endogamous blocks, these two (2) bicomponents are connected in the P-graph by a single node, P12. If they were, however, connected by two nodes, they would be recognized as one bicomponent and thus, one alliance. Moreover, if a wolf pair from Alliance 4 were to relink the pairing of one of the Alliance 1 pairs, these alliances would merge.

The project's next line of inquiry is examining the formation of these alliances through time. Time is represented in generations in the P-Graph drawings (Figures 9 and 11). In the case of this wolf data set, time, rather than generation, may be a more accurate chronology. First, not as much time passes between a wolf's parents' mating and her/his own mating as it does in human societies; wolves reach sexual maturity in only about two years. Secondly, in these data it is very common for a wolf to pair again with another mate after his/her children have done so. For these data, then, it seems useful to re-order the P-Graph drawing by date of pairing. Figure 14 is a re-drawing of the P-Graph in Figure 9. As in Figure 9, the blue nodes and arcs represent pairs involved in relinkings, and the relations between them.

Figure 15 is a similar drawing of only the allied pairs. The nodes and arcs are colored red, gray, green, and blue to represent Alliances 1, 2, 3, and 4. The next drawing, Figure 16, shows the relations between allied packs. This is essentially the same drawing as Figure 15, but reproductive units (packs) which were previously represented by multiple nodes in Figure 15 are represented with only one (1) node in Figure 16. For example, P9, P10, and P11 in Figure 15 are represented simply as 'Rose 2' in Figure 16. P9, P10, and P11 are Rose Creek's second reproductive unit comprised of 8M and three (3) Rose Creek females.

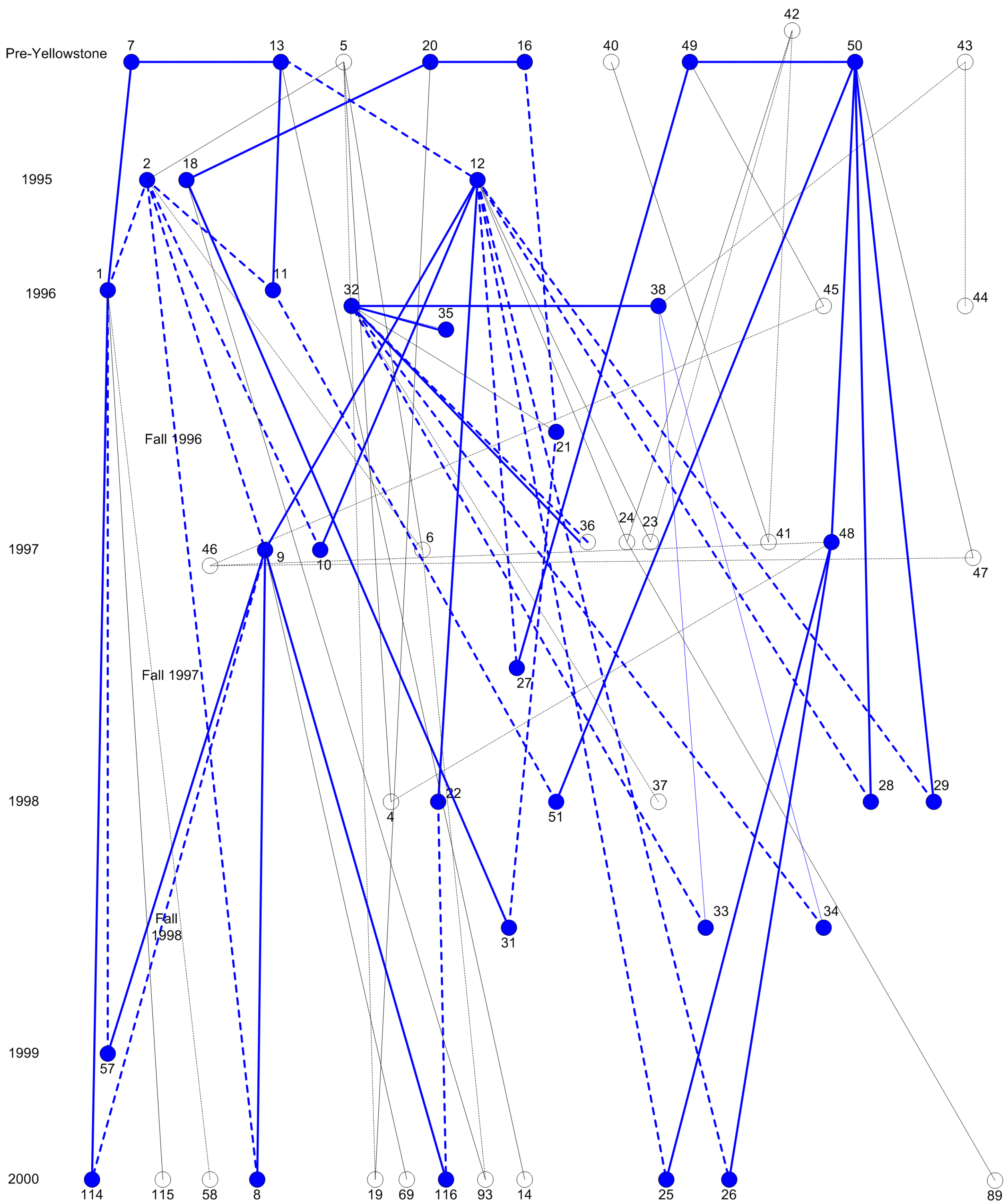

Figure 14: P-Graph Re-Ordered by Dates of Pairing Showing Relinked Pairs
Blue indicates relinking among wolf pairs.

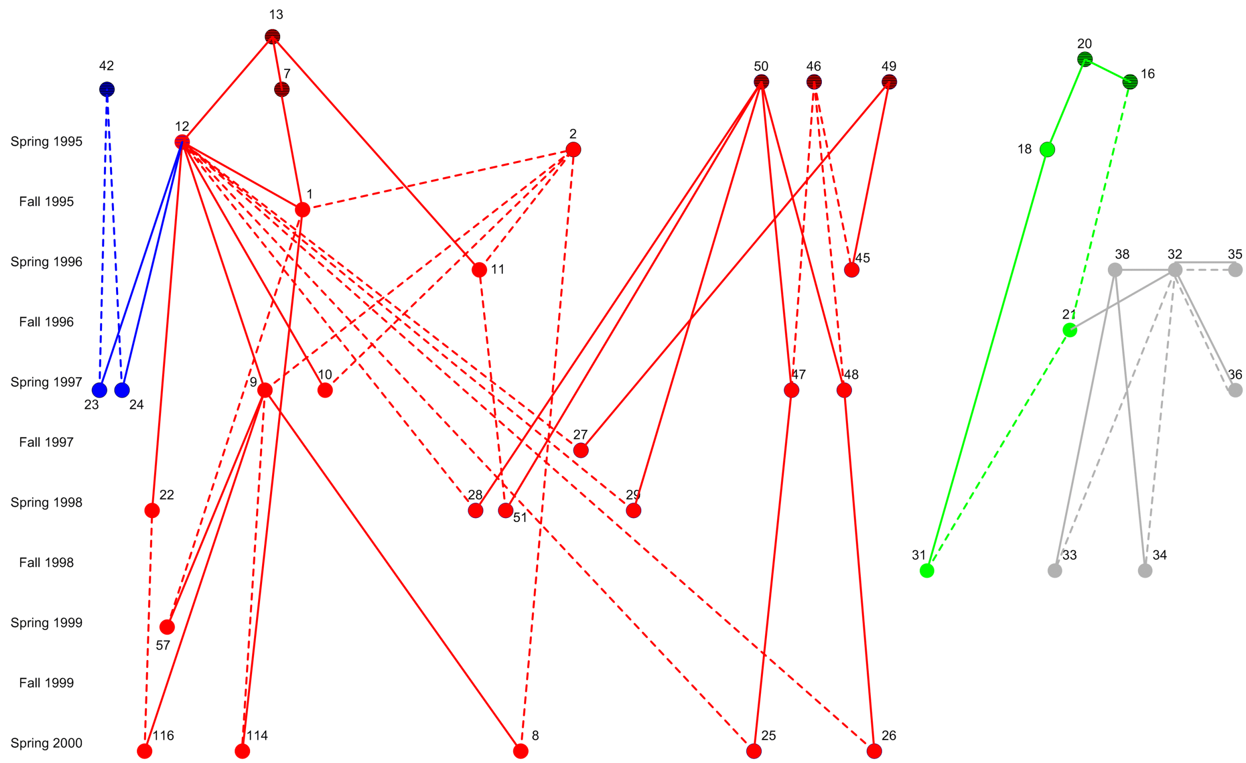

Figure 15: Mating Alliances among Pairs of Yellowstone Wolves, 1995-2000
Color denotes alliance membership: Red=Alliance 1; Gray=Alliance 2; Green=Alliance 3; Gray=Alliance 4.
Black nodes represent proxy pairs.

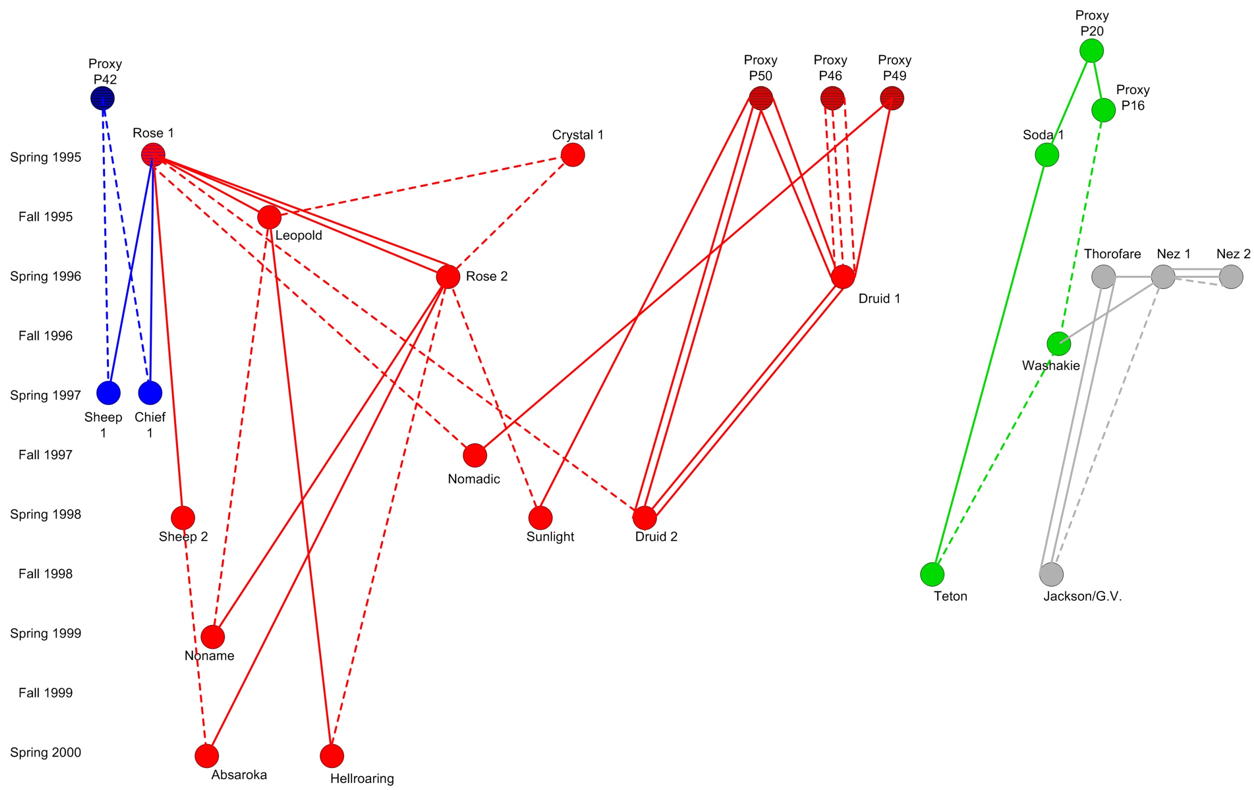

Figure 16: Mating Allliances among Packs of Yellowstone Wolves, 1995-2000

Color denotes alliance membership: Red=Alliance 1; Gray=Alliance 2; Green=Alliance 3; Gray=Alliance 4.

Table 7 provides a look at the formation of mating alliances among packs through time. Letters in parentheses (see Table 7) represent the clusters/generations of males. Table 7 uses the same notation of underlining and italics for harem arrangements as Table 5. Each of the three mating alliances is multigenerational. Interestingly, Alliances 1 and 2 include polygynous groupings within their core, originally translocated, packs (Rose & Druid in Alliance 1 and Nez in Alliance 2).

Table 7 shows that in 1996 Rose Creek, Leopold, and Crystal Creek Packs belong to Alliance 1. Also in 1996, an intrapack relinking within the Nez Perce Pack forms Alliance 2. Soda Butte, Chief Joseph, Druid Peak, Lonestar, Thorofare, and Washakie packs do not belong to any alliance. By 1997, Rose Creek, Leopold, Crystal Creek, Druid Peak, and Sunlight Basin

Packs all belong to Alliance 1. Chief Joseph and Sheep Mountain I belong to Alliance 4. Soda Butte, Thorofare, and Washakie Packs do not belong to any alliance. By 1998, all packs belong to an alliance. Rose Creek, Leopold, Crystal Creek, Druid Peak, and Sunlight Basin Packs belong to Alliance 1. Nez Perce, Thorofare, and Jackson Trio/Gros Ventre belong to Alliance 2. Washakie, Teton, and Soda Butte, who in 1997, did not belong to any alliance, all belong to Alliance 3 by the end of 1998.

Table 7: Pack Mating Alliances and Generations through Time, 1996-2000

Year	Alliance 1	Alliance 2	Alliance 3	Alliance 4	Not Allied
1996	<u>*Rose (B)*</u> Leopold (B) Crystal 1 (B)	Nez 1 (A) <u>*Nez 2 (B)*</u>			Soda 1 (Unk.-A) Chief Joseph 1 (B) Druid 1 (B) Lonestar (B) Thorofare (B) Washakie (B)
1997	<u>*Rose (B)*</u> Leopold (B) Crystal 2 (B) <u>*Druid 2 (B)*</u> Sunlight (C)	<u>*Nez 2 (B)*</u>		<u>*Chief Jo.1 (B)*</u> Sheep I (A)	Soda 1 (Unk.-A) Thorofare (B) Washakie (B)
1998	<u>*Rose (B)*</u> Leopold (B) <u>*Druid 2 (B)*</u> Sunlight (C) Crystal 3 (C)	<u>*Nez 2 (B)*</u> Thorofare (B) Jackson/G.V. (B)	Washakie (B) Teton (C) Soda (A)	SheepII (A) Chief Jo. 2 (B)	
1999	<u>*Rose (B)*</u> Leopold (B) <u>*Druid 2 (B)*</u> Sunlight (C) Crystal 3 (C) Noname (C)	<u>*Nez 2 (B)*</u> Jackson/G.v. (B)	Washakie (B) Teton (C) Soda 1 (Unk.-A)	Sheep II (A) Chief Jo. 2 (B)	

Table 7 (Continued): Pack Mating Alliances and Generations through Time, 1996-2000

2000	*Rose (B)*	*Nez 2 (B)*	Washakie (B)	Sheep II (A)
	Leopold (B)	Jackson/G.v. (B)	Teton (C)	Chief Jo. 2 (B)
	Hellroar. (C)		Soda 2 (C)	
	Absaroka (B)		Soda 3 (C)	
	Druid 2 (B)			
	Sunlight (C)			
	Crystal 3 (C)			

Note: Underlined and italicized entries represent harem arrangements. Soda 1 is followed by 'Unk.-A', because this pair was not assigned to a cluster by STRAN (Batagelj 1991) (because the male in this pair had only 'proxy' links), but it is known that he is located in generation A.

Alliance and Geography

Figures 17 – 21 are maps representing the distribution of packs and alliances through geographic space. Each map designates the pack territories over the specified year and the alliance affiliations of the Yellowstone wolf packs at the end of the year. A pack's alliance affiliation is designated by the shaded color of its territory with Red, Gray, Green, and Blue representing alliances 1, 2, 3, and 4, respectively. While the maps are original productions for this project, the estimated locations of packs and groups of wolves defined as packs was obtained from information on Ralph Maughan's (1995-2001) web site.

In each map, wolf packs appear to cluster geographically in accordance with their alliance affiliation. In addition, packs of the same alliance seem more likely to tolerate each other in close proximity than are packs who do not have an alliance affiliation, with the exception of alliances 2 and 3, which do appear to tolerate each other in rather close proximity. In the year 2000, the Teton and Gross Ventre packs are in close proximity to one another, and in 1998 and 1999 the packs of Alliance 3 are positioned horizontally "in the middle" of packs in Alliance 2.

Alliance 1, the most successful alliance in terms of total wolf numbers, has the greatest overlap in the territories of packs within its alliance, and very little territory that appears to buffer against the territory of another alliance. In addition, their territory is highly stable, contiguous, and in a constant state of growth; in each year a bounded region can easily be discerned that appears to be clearly under the control of this alliance. By the year 2000, this alliance appears to geographically control a very sizable portion of the territory in Yellowstone National Park.

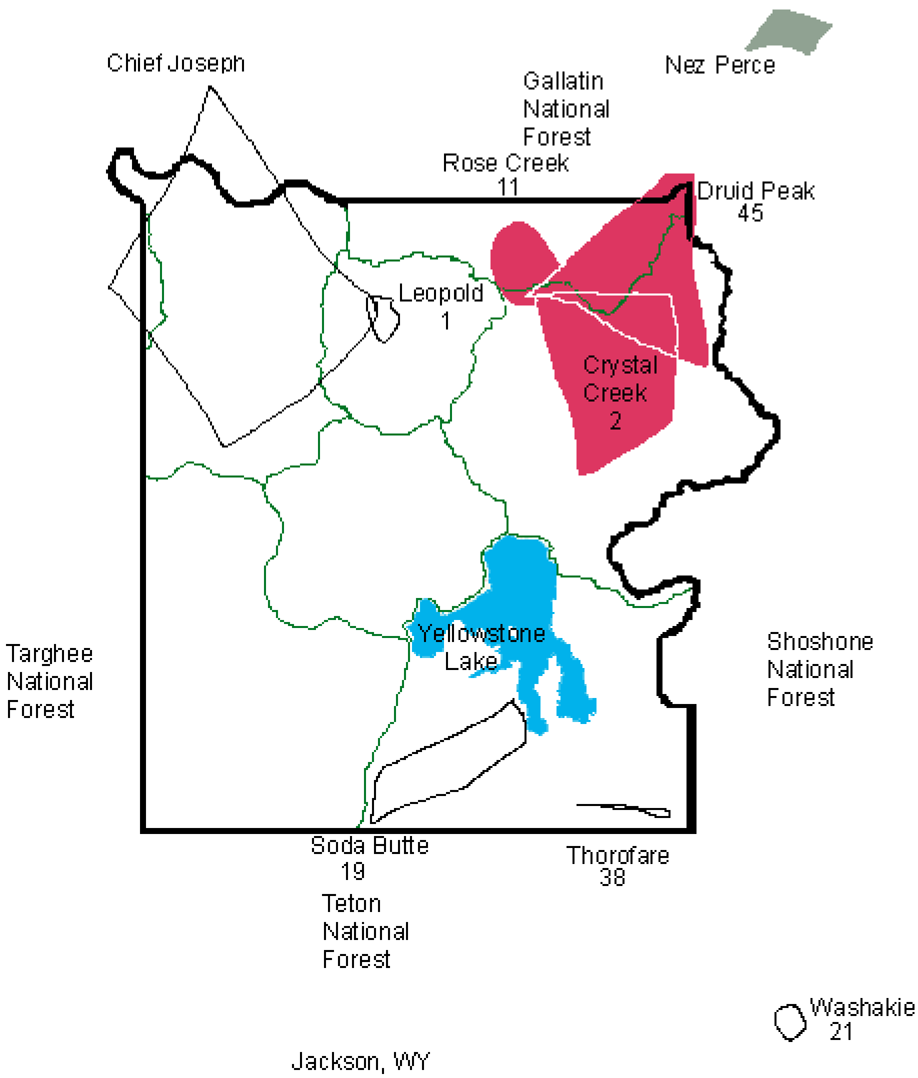

Figure 17: Map of Wolf Pack's Territory in YNP, December 1996
Color denotes alliance membership: Red=Alliance 1; Gray=Alliance 2; Green=Alliance 3; Gray=Alliance 4.
Pack areas outlined only in black represent non-allied packs.

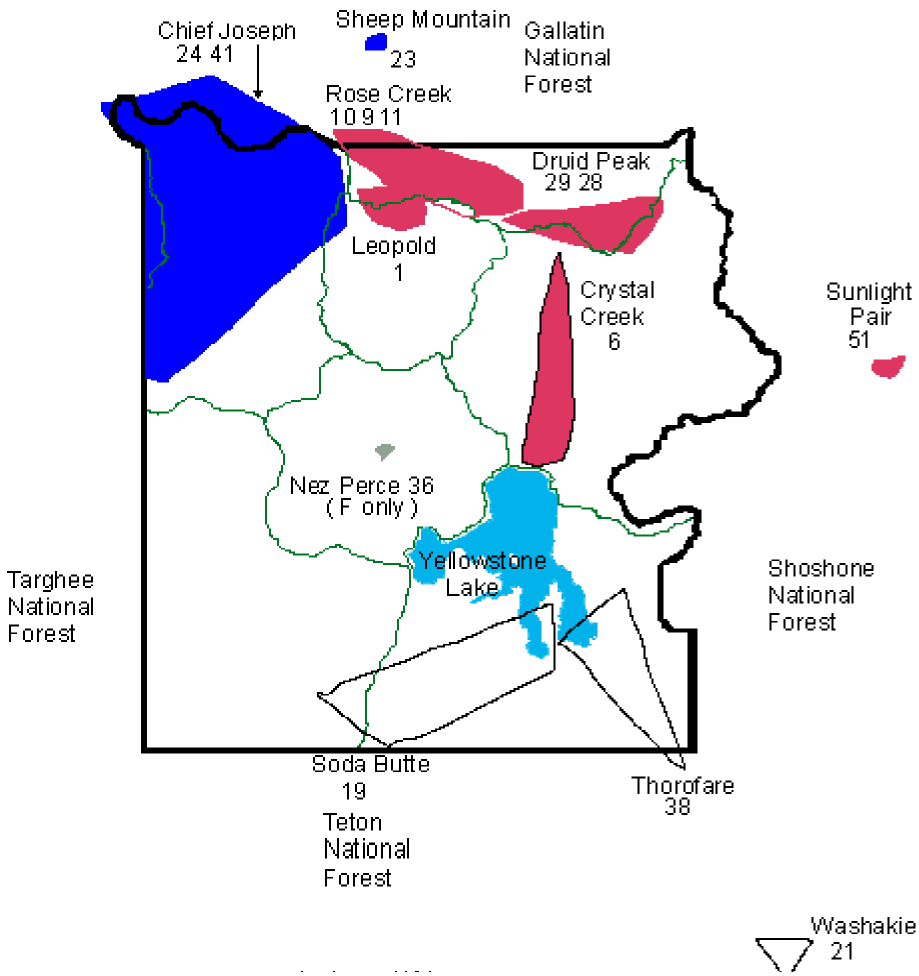

Figure 18: Map of Wolf Pack's Territory in YNP, December 1997
Color denotes alliance membership: Red=Alliance 1; Gray=Alliance 2; Green=Alliance 3; Gray=Alliance 4.
Pack areas outlined only in black represent non-allied packs.

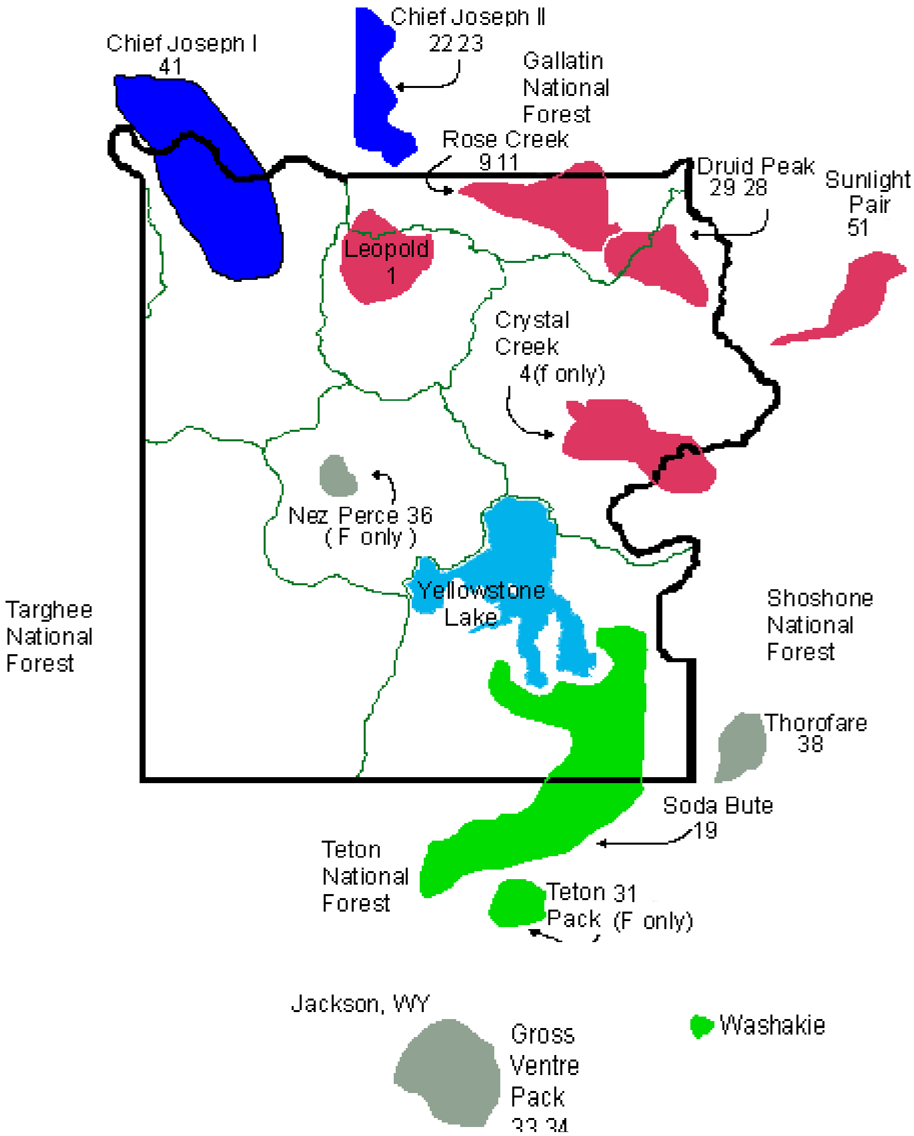

Figure 19: Map of Wolf Pack's Territory in YNP, December 1998
Color denotes alliance membership: Red=Alliance 1; Gray=Alliance 2; Green=Alliance 3; Gray=Alliance 4.
Pack areas outlined only in black represent non-allied packs.

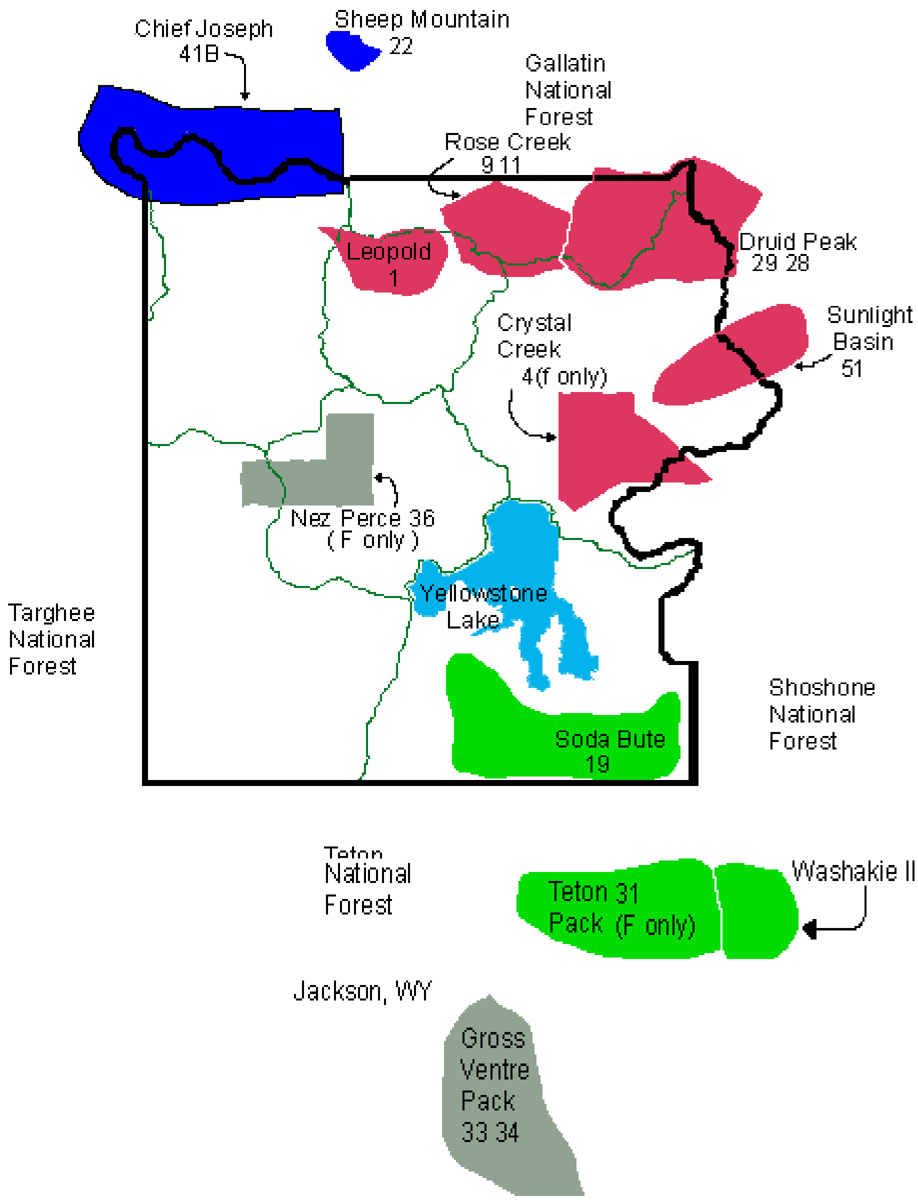

Figure 20: Map of Wolf Pack's Territory in YNP, December 1999
Color denotes alliance membership: Red=Alliance 1; Gray=Alliance 2; Green=Alliance 3; Gray=Alliance 4.
Pack areas outlined only in black represent non-allied packs.

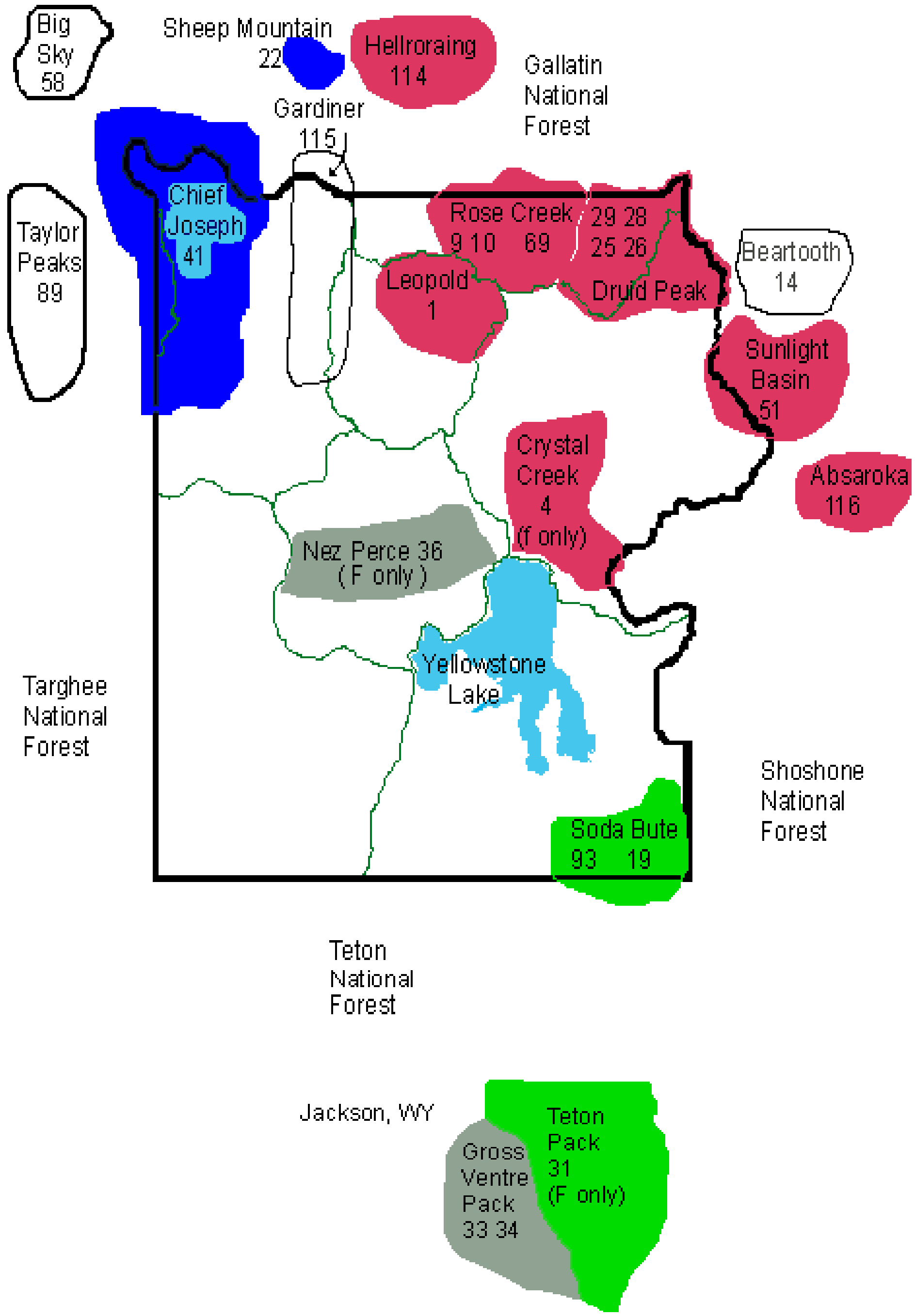

Figure 21: Map of Wolf Pack's Territory in YNP, December 2000
Color denotes alliance membership: Red=Alliance 1; Gray=Alliance 2; Green=Alliance 3; Gray=Alliance 4.
Pack areas outlined only in black represent non-allied packs.

Relational Events

The next set of analyses represent an examination of all known interpack relational events as contextual reference for the emergence of mating alliances. Sociograms of interpack events are constructed for each of the following years: 1995-1996, 1997, 1998, 1999, and 2000, followed by a set of sociograms of inter-alliance relational events.

While the analyses of the kinship data provide a final accounting of the process of alliance formation, they do not provide an accounting of the sequence of interpack events leading to the formation of alliances. It is in this way that the data regarding breeding migrations and interpack in-law relationships represented in the sociograms are distinctly different from those contained in the kinship data. Strictly speaking, however, only the non-mating data and the first category (failed courtship attempts) of the mating events data may be accurately viewed and correctly interpreted as contextual references for the mating alliance structure.

Graphical Coding of Relational Events in the Sociograms

Through the use of color, line texture, and lines directed with arrows, the sociograms differentiate among relational events on the bases of event category, quality of event, and direction (sender and recipient) of the event, respectively. Color indicates event category: green is used for failed courtship attempts; pink for breeding migrations; aqua for interpack in-law events; blue for non-breeding migration; red for fighting; gray for visitation of territory; and black is used to indicate that wolves were observed together. Solid or dashed line texture is used to indicate whether the quality of event is positive/neutral or negative. There are two negative event categories (indicated by a dashed line): 1) fighting and 2) the failed courtship attempt, which indicates that a wolf has been rejected. Positive or neutral event categories (indicated by a solid line) include all other event categories. Arrows indicating direction of events are used whenever direction is known. Event categories for which arrows are used include breeding migration, non-breeding migration, failed courtship attempts, fighting, and visitation of territory. In all cases, the recipient of the arrow is the recipient of the event. Examples include: the pack receiving a pink arrow (attached to a solid pink line) receives a breeding immigrant; the pack receiving a green arrow (attached to dashed green line) has a member who is the recipient of rejection in a failed courtship attempt; and the pack receiving a red arrow (attached to a dashed red line) is the recipient of an attack. For an event unique to the 2000 sociogram, a special graphical code is employed. The dotted and dashed line is used in conjunction with a pink line and arrow to indicate that a unique breeding migration has occurred. In this breeding migration, the migrant becomes the recipient pack's second, concurrent breeding male.

Each of the interpack sociograms also indicates which packs belong and do not belong to alliances. A pack's alliance (1, 2, 3, 4, or '0' for none) is displayed inside each pack's node. In addition, a pack's node is outlined the color designated for the alliance to which it belongs. Alliance colors are consistent with those used in previous analyses: red for Alliance 1; gray for Alliance 2; green for Alliance 3; and blue for Alliance 4. To assist the reader, the graphical codes are provided beneath each of the sociograms. In addition, an associated text table follows each sociogram providing a listing of all relational events included in the corresponding sociogram.

Time in the Sociograms

The sociograms are neither constructed as strict cross-sectional representations of relational events for each year, nor as true longitudinal representations of such events. Rather, each year represents the most recent and known relational events among the packs. When a new relational event between two packs occurs, the new event replaces the previous. For directed relational events, arrows with only colored outlines and solid colored arrows distinguish between past and current events, respectively. Directed events appear as solid arrows for years in which they occur and as outlined arrows in all subsequent years. In addition to displaying relational events, the sociograms, through the use of color, demonstrate which packs belong to specific alliances and which do not at the end of each year. While the sociograms represent a useful way to visualize complex sets of relational events among the wolves, taken alone, the sociograms may also introduce some unintended confusion. Since each sociogram displays all of the (most recent) relational events for a year as well as alliance membership at the end of each year, interpack events that happen prior to a pack's belonging to an alliance, during the year that it allies, will appear the same as events that occurred after that pack became allied. This potential for confusion exists only during the year in which a pack allies. To alert the reader to these situations, nodes for packs allying in a given year are shaded bright yellow in that year's interpack sociogram.

A Chronology of Interpack Events

1995-1996

Relations for 1995 and 1996 are presented as one graph because the only observed interpack relation in 1995 was between Crystal Creek and Rose Creek Packs, as indicated by the directed, pink line between the two packs shown in Figure 22. (The arrow, only outlined in pink, demonstrates that this is from a year prior to 1996.) In 1995, the breeding male in the Rose Creek pack is shot and killed. The Rose Creek female and her pups are placed in the Rose Creek acclimation pen and cared for by humans to ensure their survival. A Crystal Creek male is frequently observed visiting the wolves in the Rose Creek pen. When the Rose Creek female and her pups are released, the Crystal Creek male joins the Rose Creek wolves on their territory.

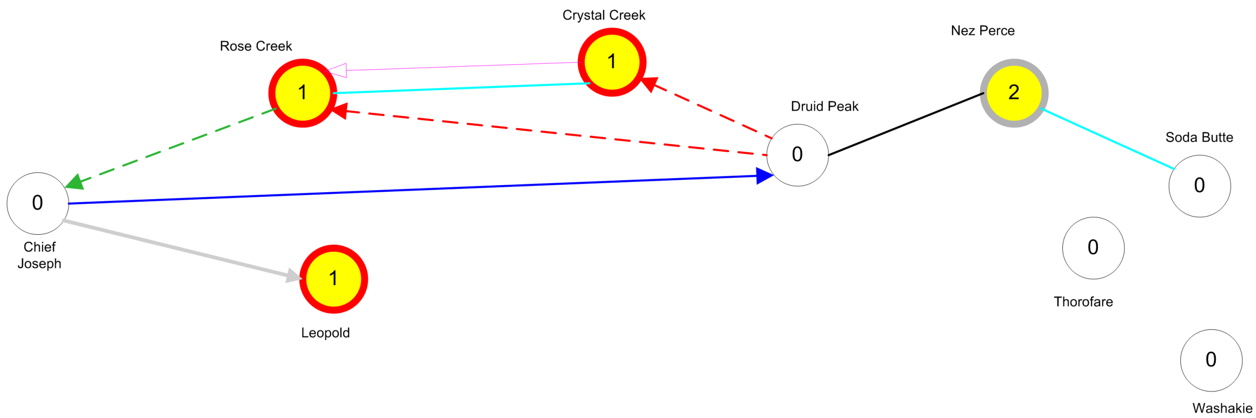

Figure 22: Known Interpack Relations at the End of 1996

Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Recipient of Gray Arrow=Recipient of territory visitation. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.

Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions. Pack nodes with yellow centers are new to alliances. Solid arrow indicates a current event. Outlined arrow indicates event from a previous year.

Table 8: Categories of 1996 Interpack Events by Type

Mating Events

Failed Courtship Attempts

1996 Chief Joseph male is chased and injured by Rose Creek wolves.

Breeding Migration

1995 Crystal Creek male, 8M, migrates to Rose Creek pairing with 9F (Replaces 10M)

'In-Laws' via Formation of a New Pack

1996 Rose Creek Female, 7F, pairs with Crystal Creek male, 2M, to form the Leopold Pack.
1996 Soda Butte male, 15M, pairs with Nex Perce female, 36F, to form the Washakie Pack.
1996 Former Lonestar male, 35M, pairs with Nez Perce female, 30F, to form the Thorofare Pack.*

Non-Mating Events

Non-breeding migration

1996 Chief Joseph male migrates to the Druid Peak pack.
1997 34M's mate, 16F, migrates from Chief Joseph to den alone in Chief Joseph II.

Fighting

1996 Druids attack Rose Creek wolves.
1996 Druids attack Crystal Creek wolves.

Observed playing or eating together

1996 Druid female, 39F, is observed with pups believed to be Nez Perce female 27F's displaced pups.

Table 8 (Continued): Categories of 1996 Interpack Events by Type

Visits Territory	
1996	Two Chief Joseph males visit the Leopold's densite while the Leopold Pack is away.

Underline indicates that breeding wolf of same sex as suitor is present in rejecting pack or pack receiving the immigrant wolf. *Is not represented in the sociograms as an in-law event. In 1995, Lonestar dissolved when its only other member, 35M's mate, died. The in-law event is not represented, because the Lonestar Pack is not represented.

In 1996, the Leopold pack is formed when a Rose Creek female and a Crystal Creek male pair and establish territory near Rose Creek (see map in Figure 17). The formation of the Leopold pack creates an in-law tie between the Rose Creek and Crystal Creek Packs. Three packs belong to Alliance 1: Rose Creek, Leopold, and Cyrstal Creek. Interestingly, there are no known interpack relational events occurring between the Leopold Pack and either of its two allies. The mating events between the Rose Creek and Crystal Creek packs, a breeding male migration from 1995 and an interpack, in-law event, are the mating events which have generated the alliance among all three of the packs.

The only other belonging to an alliance is the Nez Perce Pack. Oddly, this alliance, Alliance 2, begins as an intrapack alliance. Recall that Nez Perce wolf, 29M, pairs with his sister and that this is the only YNP pack in the study period in which a breeding male resides on his natal pack's territory.

In the spring of 1996 the door to the pen holding the newly translocated Druid Peak pack is opened, but the wolves do not exit the pen for twelve days. Within the first two and one half months of their release, the Druids attack both the Rose Creek and Crystal Creek packs. In October, 1996 Druid female 39F disperses, leaving behind her daughters and the male wolf with whom she was penned. She travels far outside of Yellowstone and then returns to YNP, but not to the Druids (during 1996). She is observed with two pups believed to be the displaced pups of

Nez Perce female #27F. (This observation is represented by the black tie between the Druid Peak and Nez Perce nodes in Figure 22.)

Also in 1996, two Chief Joseph males visit the Leopold's densite while the Leopold Pack is away from home. One of these two visiting Chief Joseph Pack males migrates (as a non-breeding male) to the Druid Peak Pack. The other Chief Joseph male executes a failed courtship attempt near the Rose Creek pack where he is chased and injured by Rose Creek wolves.

Pack interaction in the southern portion of YNP during 1995-1996 centers around pack formation. The non-allied Soda Butte pack, released in 1995, and the 1996-released Nez Perce pack develop an in-law tie when the Washakie Pack forms and establishes territory far to the south and east of their natal packs (see Figure 17). The Lonestar pack of two wolves dissolves about one (1) month after its release, when the female, 36F, falls into a geyser and dies. The male, however, soon finds a mate from the Nez Perce Pack and together they form the Thorofare Pack, establishing territory in the southeast corner of YNP not far from the Soda Butte pack. (Because of its brief existence, the Lonestar Pack does not appear in Figures 17 or 22.)

1997

Figure 23 shows that four more packs are now allied. Chief Joseph and Chief Joseph II /Sheep Mountain belong to the newly formed Alliance 4. The Chief Joseph male, who was previously injured by the Rose Creek Pack, appears near their territory again during 1997. This time two females, 16F and 17F, follow him. He is observed in a physical mating tie with both females, but establishes territory with and tends to the densite of only one, 17F, who dens on Chief Joseph territory (see Figure 18). The other female, 16F, dens alone just north and east of the Chief Joseph territory, not from her natal Rose Creek territory (see Figure 18). (The area where 16F dens is referred to as Chief Joseph II, until she dens again on that same territory after pairing with a new (live-in) mate and the pack is renamed, Sheep Mountain Pack.)

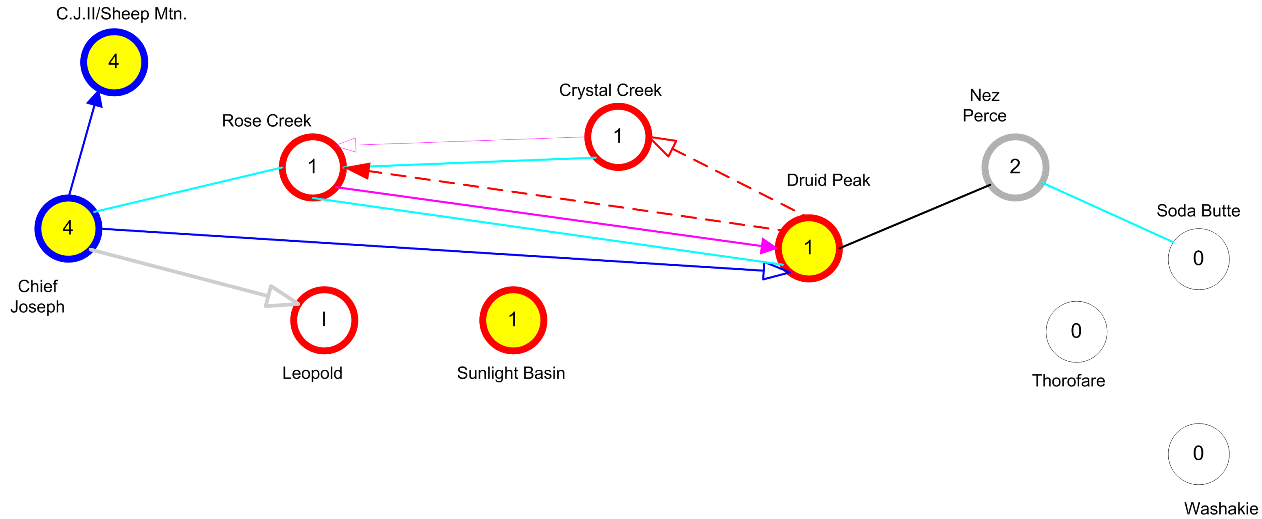

Figure 23: Known Interpack Relations at the End of 1997
Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Recipient of Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.
Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions. Pack nodes with yellow centers are new to alliances. Solid arrow indicates a current event. Outlined arrow indicates event from a previous year.

Table 9: Categories of 1997 Interpack Events by Type

Mating Events

Failed Courtship Attempts
None

Breeding Migration
1995 Crystal Creek male, 8M, migrates to Rose Creek pairing with 9F (Replaces 10M)
1997 Rose Creek male, 21M migrates to Druid Peak Pack.

'In-Laws' via Formation of a New Pack
1996 Rose Creek Female, 7F, pairs with Crystal Creek male, 2M, to form the Leopold Pack.
1996 Soda Butte male, 15M, pairs with Nex Perce female, 36F, to form the Washakie Pack.
1997 Chief Joseph II is formed when 16F of Rose Creek pairs with Chief Joseph 34M, but dens alone.
1997 Rose creek male pairs with Druid Peak female, forming the Sunlight Basin Pack.

Non-Mating Events

Non-breeding migration
1996 Chief Joseph male migrates to the Druid Peak pack.
1997 34M's mate, 16F, migrates from Chief Joseph to den alone in Chief Joseph II.

Table 9 (Continued): Categories of 1997 Interpack Events by Type

Fighting
1996 Druids attack Crystal Creek wolves.
1997 Druids invade Rose Creek killing 19F and her pups.

Observed playing or eating together
1996 Druid female, 39F, is observed with pups believed to be Nez Perce female 27F's displaced pups.

Visits Territory
1996 Two Chief Joseph males visit the Leopold's densite while the Leopold Pack is away.

The other two packs that become allied in 1997 are the Druid Peak Pack and the newly formed Sunlight Basin Pack. Both packs now belong to Alliance 1. During 1997, both Druid males die in two separate shooting incidents. A male from the Rose Creek pack moves in as the Druid's new breeding male. Just prior to his immigration to the Druid's, he pairs briefly with the wandering Druid female 39F. Another Rose Creek male pairs with a Druid female, establishing territory in the Sunlight Basin area (see map in Figure 18) near the Druid Peak pack. This new pack, also belonging to Alliance 1, is called the Sunlight Basin Pack. The 1997 attack of Rose Creek 19F and her pups by the Druid Peak wolves happened prior to the breeding migration of Rose Creek 21M to the Druid Peak Pack; and thus, at a time when the Druid Peak Pack did not belong to Alliance 1. After the breeding migration of 21M and the formation of the Sunlight Basin Pack, there is no fighting observed among wolf packs in the northern portion of the park until 1999 when the yearling males of the dissolving Crystal Creek Pack attack the Druid Peak Pack.

1998

By the end of 1998 five (5) more packs are in two different mating alliances in when two new packs form in the southern portion of the YNP (see Figure 24). Thorofare Pack and the Jackson Trio/Gros Ventre Pack become part of Alliance 2, to which previously only the Nez

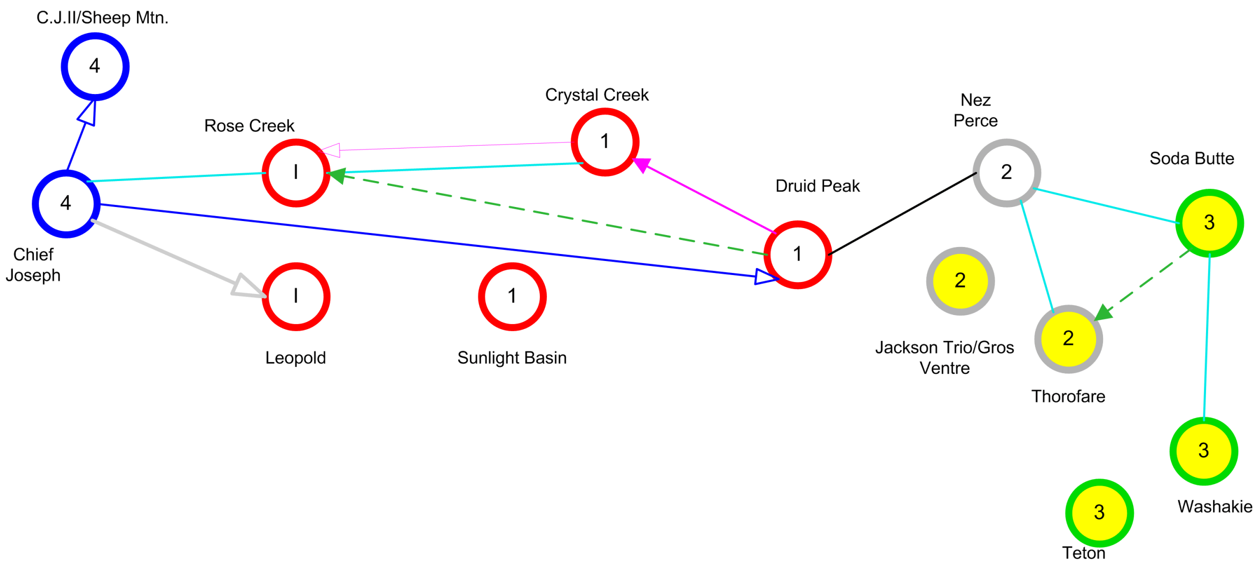

Figure 24: Known Interpack Relations at the End of 1998

Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Recipient of Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.

Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions. Pack nodes with yellow centers are new to alliances. Solid arrow indicates a current event. Outlined arrow indicates event from a previous year.

Table 10: Categories of 1998 Interpack Events by Type

Mating Events

Failed Courtship Attempts

<u>1998 Rose Creek female is killed on Druid territory.</u>**

1998 Thorofare male is killed by Soda Butte Pack.

Breeding Migration

1995 Crystal Creek male, 8M, migrates to Rose Creek pairing with 9F (Replaces 10M)

1998 Druid Peak male 104M migrates to Crystal Creek Pack.

'In-Laws' via Formation of a New Pack

1996 Rose Creek Female, 7F, pairs with Crystal Creek male, 2M, to form the Leopold Pack.

1996 Soda Butte male, 15M, pairs with Nex Perce female, 36F, to form the Washakie Pack.

1997 Chief Joseph II is formed when 16F of Rose Creek pairs with Chief Joseph 34M, but dens alone.

1998 Washakie male, 133M, pairs with Soda Butte female, 24F, to form the Teton Pack.

1998 Two females form the Thorofare pack pair with Nez Perce male, 29M to form the Gros Ventre Pack.

Non-Mating Events

Non-breeding migration

1996 Chief Joseph male migrates to the Druid Peak pack.

1997 34M's mate, 16F, migrates from Chief Joseph to den alone in Chief Joseph II.

Fighting

None

Table 10 (Continued): Categories of 1998 Interpack Events by Type

Observed playing or eating together
1996 Druid female, 39F, is observed with pups believed to be Nez Perce female 27F's displaced pups.

Visits Territory
1996 Two Chief Joseph males visit the Leopold's densite while the Leopold Pack is away.

Underline indicates that breeding wolf of same sex as suitor is present in rejecting pack or pack receiving the immigrant wolf. ** This is the only case failed courtship attempt of a female suitor.

Perce Pack belonged when two females from the Thorofare Pack pair with a Nez Perce male to form the Jackson Trio/Gros Ventre pack. An in-law event occurs between the Soda Butte and Washakie Packs when the Teton pack is formed. All three packs: Soda Butte, Washakie, and Teton Packs now belong to Alliance 3. Also in the southern portion of the park during 1998, the breeding female of the Thorofare Pack was killed in an avalanche leaving the Thorofare male without a mate during mating season. Shortly after the death of his mate, the Thorofare male is rejected (killed) by the Soda Butte Pack. The Thorofare Pack pups (born in 1997) are left alone to fend for themselves. During 1998 the breeding female of the Washakie pack and the single mother of the Washakie pups is killed for livestock depredation leaving the Washakie pups to survive on their own.

In the northern portion of YNP, the Crystal Creek Pack's breeding male, 6M, is killed while hunting. Shortly after, the Druid Peak pack travels near the Crystal Creek territory and Druid 104M disperses to become the breeding male of the Crystal Creek Pack. During the 1998 mating season, a female from the Rose Creek pack travels into Druid Peak Pack's Territory and is killed.

1999

In 1999, a new pack is formed when a Rose Creek female and a Leopold male pair establishing territory near the Rose Creek Pack's territory. This pack is referred to as the

'Noname' pack, because the breeding female is shot before the pack was officially named. The formation of the Noname Pack creates an in-law event between the Rose Creek and Leopold Packs; thus, the Noname Pack also belongs Alliance 1.

Figure 25 shows that numerous interpack relational events occurred in 1999. The Soda Butte Pack, located in the southern portion of YNP is involved in the majority of these interactions. During the 1999 mating season, a Soda Butte male is frequently observed near Rose Creek territory interacting with Rose Creek females, and howling at the pack, but eventually returns home without a mate. In the fall of 1999, 104M leaves the Crystal Creek pack to join the Soda Butte Pack. Crystal Creek male 120M follows 104M and becomes a breeding male in the Soda Butte Pack.

In the northern portion of YNP, Crystal Creek breeding female, 5F, disperses from Crystal Creek leaving behind a group of yearling males. Not long after her dispersal, this group of yearling males attacks the Druids, invading their territory and killing a pup. One of these Crystal Creek males joins the Chief Joseph pack. Shortly after, three unidentified gray males (of unidentified origin) also appear to have migrated into the Chief Joseph pack. The original immigrant from Crystal Creek has three gray littermates. Since their identities have not been confirmed, these three immigrations do not appear in Figure 25. Also in the northern portion of YNP, a male Chief Joseph suitor is frequently tracked in the Lamar Valley, the Druid's territory. He eventually wanders home without a mate.

In the southern portion of Greater Yellowstone Area (GYA), the offspring from the defunct Thorofare and Washakie Packs merge when the Thorofare wolves migrate to the former Washakie pack's range, to become the Washakie II/Dunoir wolves.

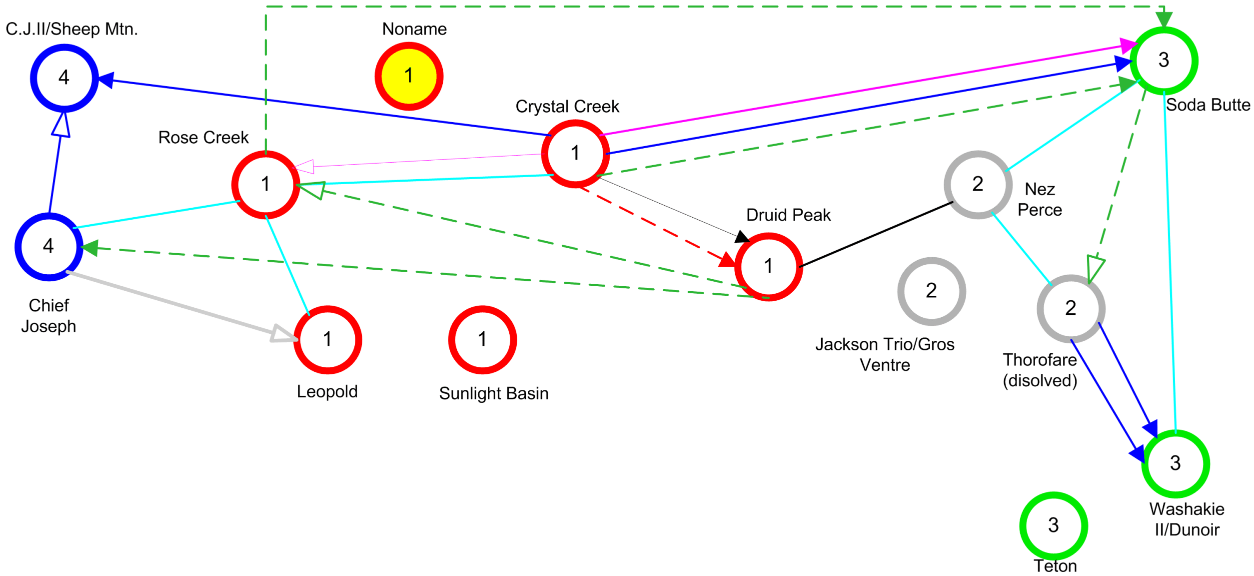

Figure 25: Known Interpack Relations at the End of 1999

Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Recipient of Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.
Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions. Pack nodes with yellow centers are new to alliances. Solid arrow indicates a current event. Outlined arrow indicates event from a previous year.

Table 11: Categories of 1999 Interpack Events by Type

Mating Events

Failed Courtship Attempts

<u>1998 Rose Creek female is killed on Druid territory.</u>
1998 Thorofare male is killed by Soda Butte Pack.
<u>1999 Soda Butte male is repeatedly ignored by Rose Creek Pack.</u>
<u>1999 Chief Joseph male is rejected by Druids.</u>
<u>1999 Soda Butte male is killed by Crystal Creek Pack.</u>

Breeding Migration

1995 Crystal Creek male, 8M, migrates to Rose Creek pairing with 9F (Replaces 10M)
1999 Crystal Creek male 120M migrates to Soda Butte

'In-Laws' via Formation of a New Pack

1996 Rose Creek Female, 7F, pairs with Crystal Creek male, 2M, to form the Leopold Pack.
1996 Soda Butte male, 15M, pairs with Nex Perce female, 36F, to form the Washakie Pack.
1997 Chief Joseph II is formed when 16F of Rose Creek pairs with Chief Joseph 34M, but dens alone.
1998 Washakie male, 133M, pairs with Soda Butte female, 24F, to form the Teton Pack.
1998 Two females form the Thorofare pack pair with Nez Perce male, 29M to form the Gros Ventre Pack.
1999 Rose creek female pairs with a Leopold male to form the Noname Pack near the Rose Creek territory.

Table 11 (Continued): Categories of 1999 Interpack Events by Type

Non-Mating Events

Non-breeding migration

1997 34M's mate, 16F, migrates from Chief Joseph to den alone in Chief Joseph II.
1999 Crystal Creek male 104M (former Druid) migrates to Soda Butte.
1999 Crystal Creek male joins the Chief Joseph Pack II/Sheep Mtn. Pack
1999 Thorofare pups migrate to Washakie pack (becomes Washakie II).

Fighting

1999 Crystal Creek yearling males attack Druid Peak Pack.

Observed playing or eating together

1996 Druid female, 39F, is observed with pups believed to be Nez Perce female 27F's displaced pups.
1999 5F (recent disperser from Crystal Creek) observed dining with Druid Peak Pack.

Visits Territory

1996 Two Chief Joseph males visit the Leopold's densite while the Leopold Pack is away.

Underline indicates that breeding wolf of same sex as suitor is present in rejecting pack or pack receiving the immigrant wolf.

2000

In the northern portion of the GYA two new packs, the Hellroaring and Absaroka Packs, form and are part of Alliance 1 (see Figure 26). An in-law event occurs between the Rose Creek wolves and the Leopold wolves when a male from Rose Creek pairs with a female from the Leopold Pack to form the Helloaring Pack. A second in-law event occurs in 2000 when a male from the Sheep Mountain Pack pairs with a female from the Rose Creek Pack to form the Absaroka Pack.

Although no interpack aggression was observed in 2000, the wolves began attacking domestic dogs. The Chief Joseph pack, in the northeast portion of the GYA, kills four dogs. In addition four (4) wolf packs, in the southern portion of the GYA, are reported to have killed dogs, with two of the packs attacking dogs at the same ranch. Although it is difficult to say with any certainty, it seems that the wolf packs, most of whom are allied with one another are coexisting peacefully, have begun to attack nearby "rival packs" of domestic dogs.

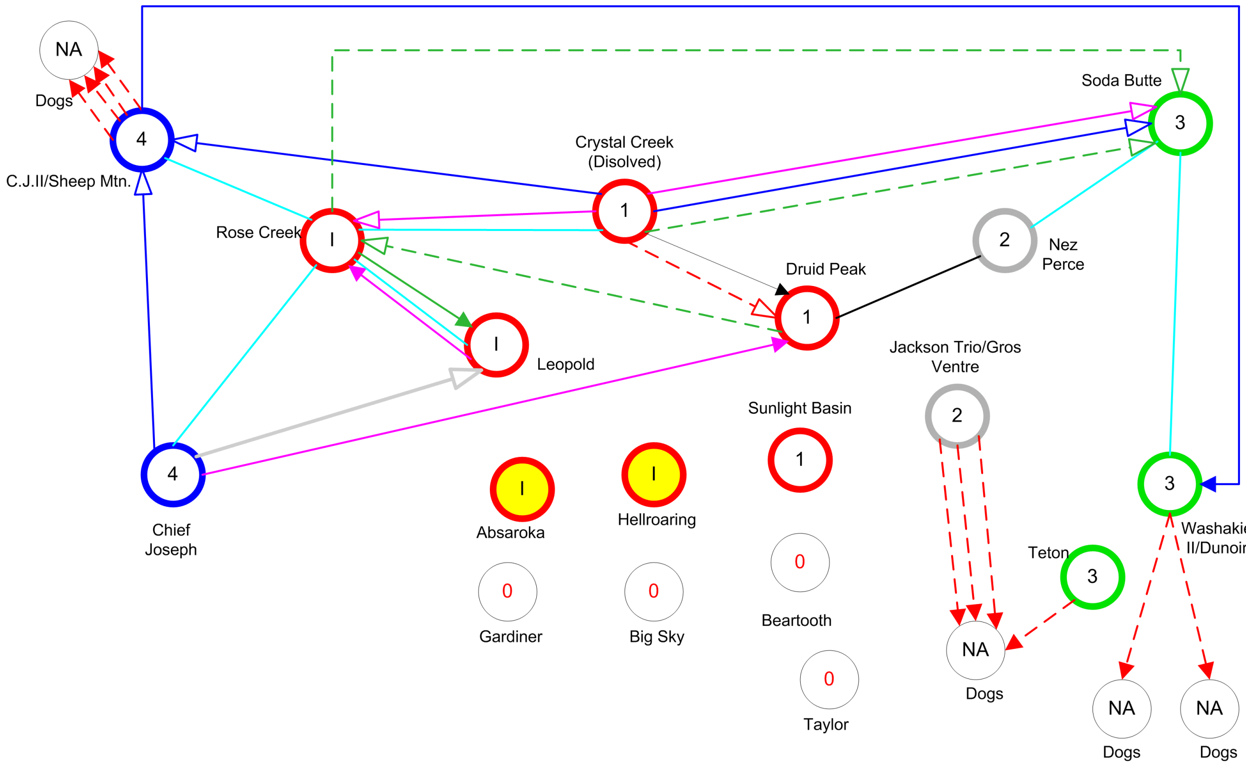

Figure 26: Known Interpack Relations at the End of 2000
Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Recipient of Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.
Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions. Pack nodes with yellow centers are new to alliances. Solid arrow indicates a current event. Outlined arrow indicates event from a previous year.

Table 12: Categories of 2000 Interpack Events by Type

Mating Events

Failed Courtship Attempts

<u>1998 Rose Creek female is killed on Druid territory.</u>
<u>1999 Soda Butte male is repeatedly ignored by Rose Creek Pack.</u>
<u>1999 Soda Butte male is killed by Crystal Creek Pack.</u>
<u>2000 Leopold male rejected by Rose Creek</u>

Breeding Migration

1995 Crystal Creek male, 8M, migrates to Rose Creek pairing with 9F (Replaces 10M).
1999 Crystal Creek male 120M migrates to Soda Butte
<u>2000 Chief Joseph male migrates to Druids as their 2nd breeding male.</u>
<u>2000 Leopold male migrates to Rose Creek as their 2nd breeding male.</u>

Table 12 (Continued): Categories of 2000 Interpack Events by Type

'In-Laws' via Formation of a New Pack
1996 Rose Creek Female, 7F, pairs with Crystal Creek male, 2M, to form the Leopold Pack.
1996 Soda Butte male, 15M, pairs with Nex Perce female, 36F, to form the Washakie Pack.
1997 Chief Joseph II is formed when 16F of Rose Creek pairs with Chief Joseph 34M, but dens alone.
1998 Washakie male, 133M, pairs with Soda Butte female, 24F, to form the Teton Pack.
1999 Rose creek female pairs with a Leopold male to form the Noname Pack near the Rose Creek territory.

Non-Mating Events

Non-breeding migration
1997 34M's mate, 16F, migrates from Chief Joseph to den alone in Chief Joseph II.
1999 Crystal Creek male 104M (former Druid) migrates to Soda Butte.
1999 Crystal Creek male joins the Chief Joseph Pack II/Sheep Mt. Pack.
2000 Chief Joseph II/Sheep Mt. male migrates to Washakie II.

Fighting
1999 Crystal Creek yearling males attack Druid Peak Pack
2000 Chief Joseph II/Sheep Mtn. Pack attacks dogs
2000 Three packs in southern YNP (Washakie/Dunoir, Teton, and Jackson/Gros Ventre) attack dogs.

Observed playing or eating together
1996 Druid female, 39F, is observed with pups believed to be Nez Perce female 27F's displaced pups.
1999 5F (recent disperser from Crystal Creek) observed dining with Druid Peak Pack.

Visits Territory
1996 Two Chief Joseph males visit the Leopold's densite while the Leopold Pack is away.

Underline indicates that breeding wolf of same sex as suitor is present in rejecting pack or pack receiving the immigrant wolf.

A new pattern regarding territory and mating is observable among packs in the northern part of the GYA in 2000. It may have begun last year with the formation of the Noname pack, which was established very near to (or possibly on?) the Rose Creek territory. Recall that the female of this pair (78F) was born a Rose Creek wolf so, if this pack formed on Rose Creek territory, this would mean that Rose Creek pack allowed another breeding male to enter the pack. This same behavior occurs again in 2000 when the Chief Joseph male, once rejected by the Druids in 1999, migrates to the Druids and appears to be in the process of coupling with one of the Druid females. It is believed that her current pups were fathered by the pack's long-standing breeding male, 21M, but she has denned separately from the rest of the pack. The Chief Joseph male is tending to her and her pups. Also in 2000, a Leopold male is initially rejected by Rose Creek wolves, but then pairs with a Rose Creek female on Rose Creek Territory. In the southern portion of the park, the new Washakie II pack has received an immigrant male from the Chief Joseph pack. It is not known whether he or any other member of this pack is breeding.

Alliances in Context

While interpack interactions are most frequently described as only hostile, findings from theses analyses of interpack relational events clearly demonstrate that interpack behavior is characterized by a wide range of interactions. In fact, interpack mating-related behaviors (such as the breeding migration and pack formation via in-law events) are so common that all packs in YNP belong to an alliance by 1998. Further, these findings suggest that the mating alliances formed have social implications beyond the mating structure to other interpack relational events such as migrations, aggression, and acceptance vs. rejection during courtship. Most interestingly, the interpack sociograms for all years show almost no fighting between allied members during any of the years, indicating that most packs allied through mating were not observed in interpack fighting once they had allied. Failed courtship attempts are also rare between packs belonging to the same alliance.

Inter-Alliance Events

Figures 27 through 31 show an aggregation of interpack relational events to an inter-alliance level. While the interpack events sociograms provided a visual display of alliance formation, such a visual aggregation of events allows for an examination of the greater context in which the alliance exists. Moreover, findings from an examination of inter-alliance event sociograms may suggest a higher level of social organization, beyond the alliance, among the wolves.

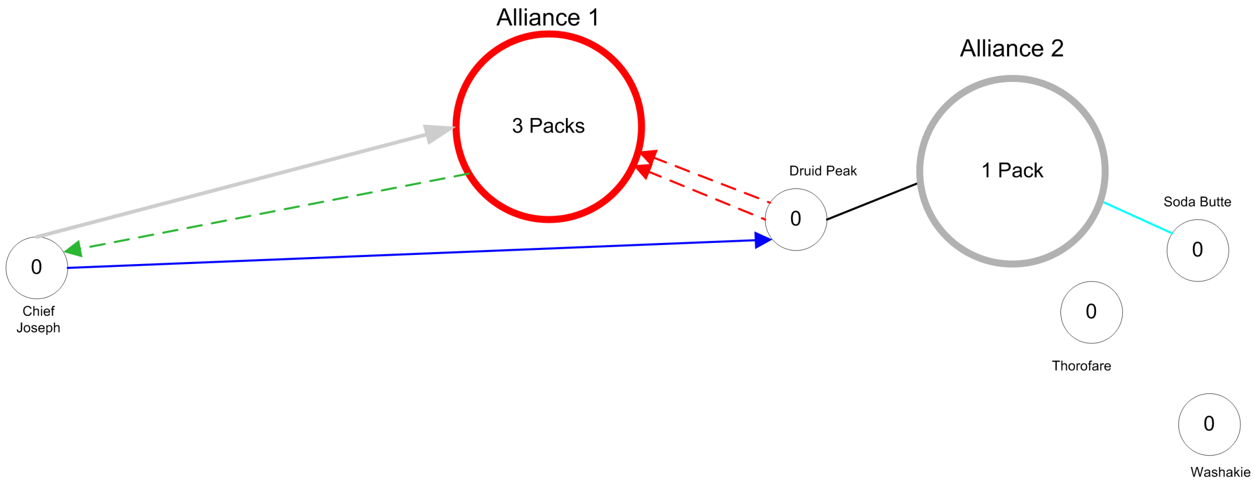

Figure 27: Relational Events between Alliances at the End of 1996
Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.
Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions.

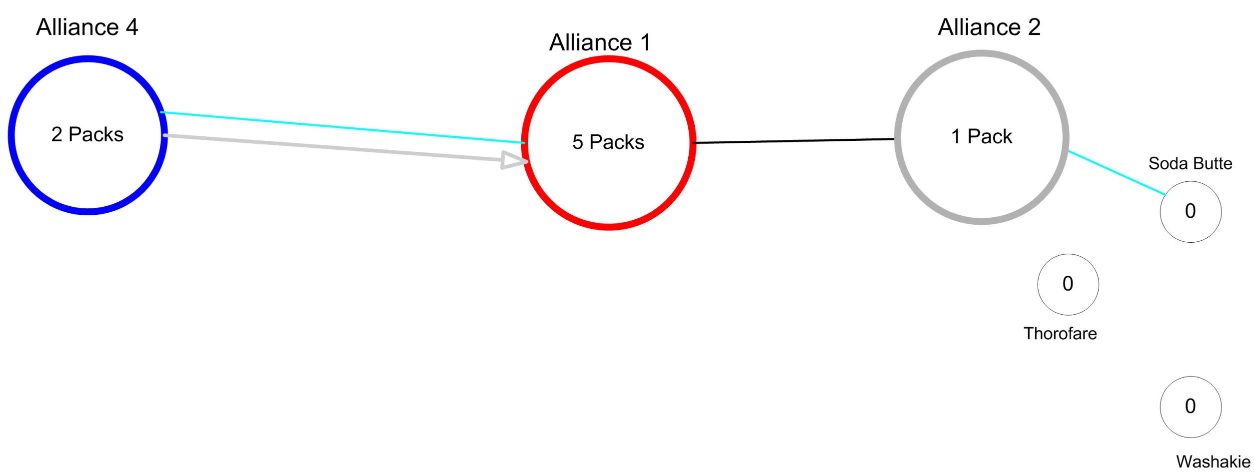

Figure 28: Relational Events between Alliances at the End of 1997
Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.
Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions.

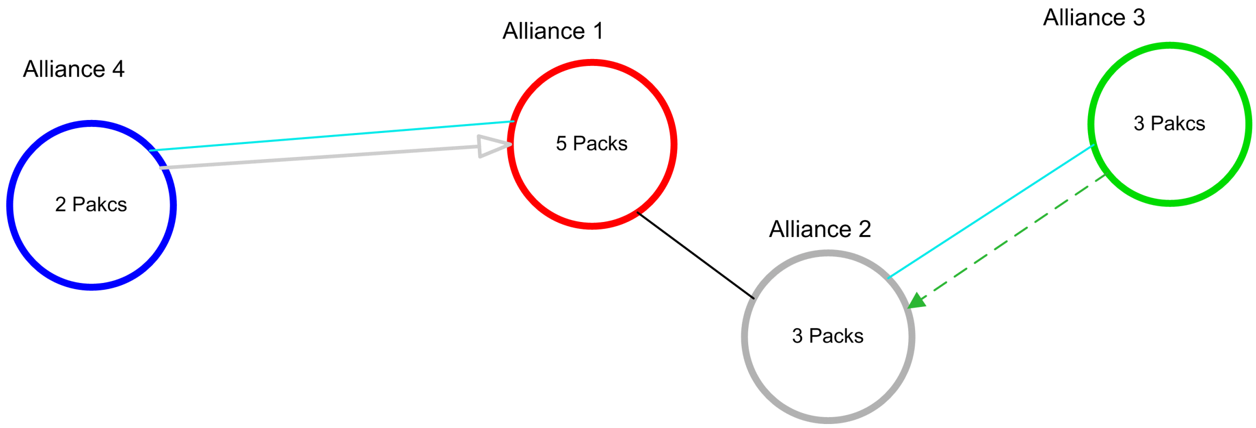

Figure 29: Relational Events between Alliances at the End of 1998
Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.
Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions.

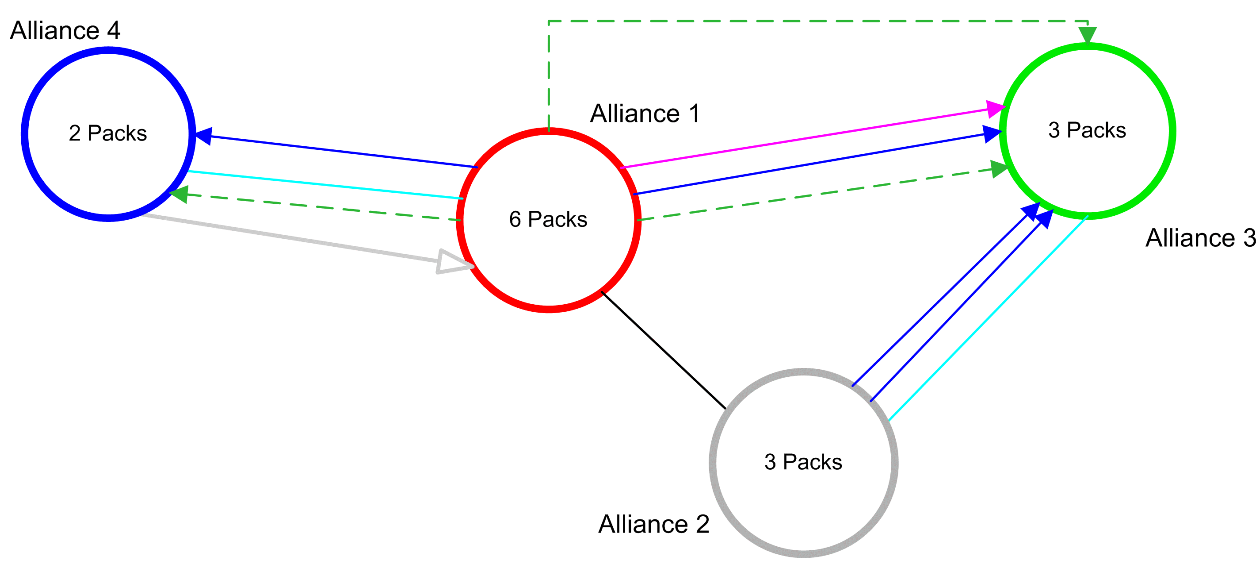

Figure 30: Relational events between Alliances at the End of 1999
Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.
Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions.

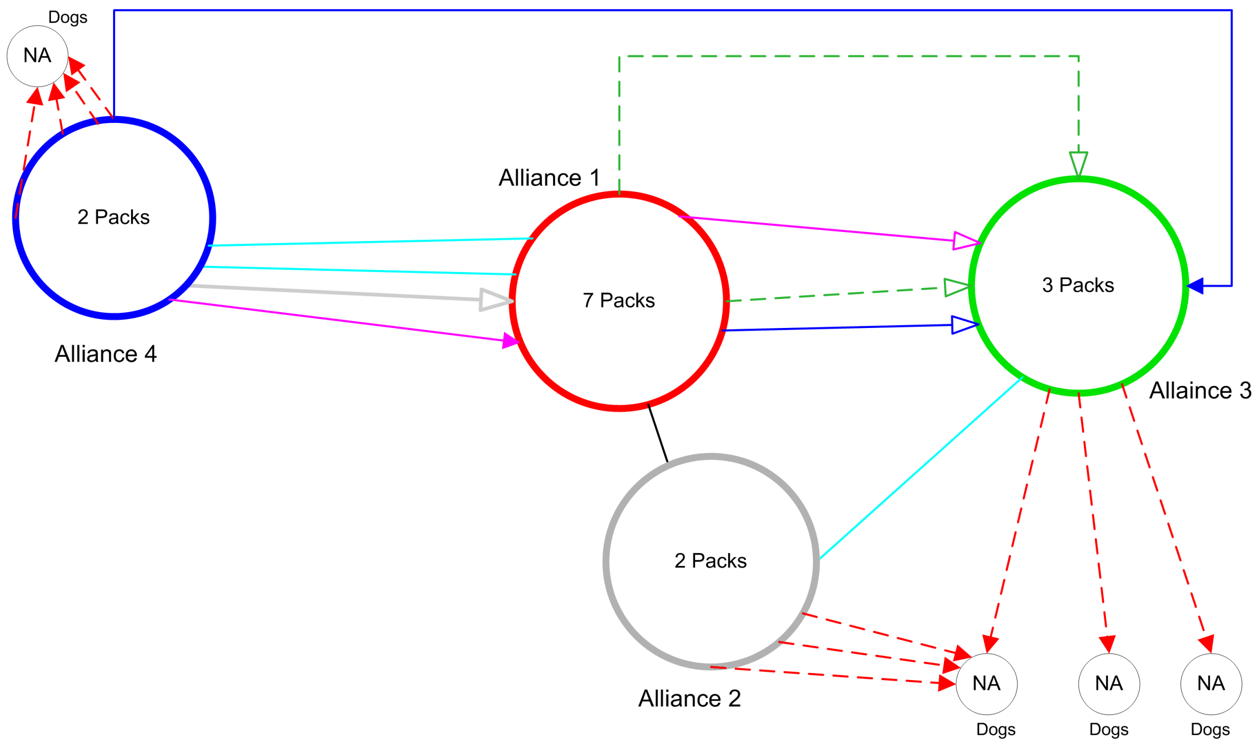

Figure 31: Relational events between Alliances at the End of 2000
Event Categories: Recipient of Blue Arrow=Recipient of immigrant from; Recipient of Pink Arrow=Recipient of breeding male from; Recipient of Green Arrow=Rejected by; Recipient of Red Arrow=Recipient of aggression from; Gray Arrow=Recipient of visits territory. Non-directed Black Event 'Tie'=Positive or neutral interaction; Non-directed Aqua Event 'Tie'=In-law relation formed due to new pack formation.
Event Quality: Sold lines represent events characterized by positive or neutral interactions. Dashed lines represent events characterized by negative or hostile interactions.

Figure 27 shows the relational events between alliances at the end of 1996. In 1996, four (4) packs belong to two (2) alliances (Rose Creek, Leopold, and Crystal Creek belong to Alliance 1 while Nez Perce belongs to Alliance 2). Five (5) packs do not belong to any alliance (Soda Butte, Chief Joseph, Druid Peak, Thorofare, and Washakie.) By the end of 1997 (see Figure 28), Alliance 3 has formed, and two packs (Chief Joseph and Sheep Mountain) belong to this alliance. Also by the end of 1997, Druid Peak belongs to Alliance 1, leaving only three packs that do not belong to any alliance (Soda Butte, Thorofare, and Washakie). By 1998, YNP wolf packs have formed four distinct mating alliances (see Figure 29). In this year (and in 1999 and 2000) all packs belong to an alliance. It is interesting to note that the majority of non-mating interpack relational events occur between allied packs, rather than between non-allied packs or between non-allied packs and allied packs. This seems to suggest that there is some relationship between alliance formation (and thus, breeding migrations and in-law events) and participation in other interpack events.

By 2000, the two northern alliances share two affinal ties and the two southern alliances one affinal tie, but there are no affinal ties between the northern and southern groups. Moreover, wolf packs in the two southern alliances (Alliance 2 and Alliance 3) appear to form a coalition against groups of domestic dogs owned by neighboring ranchers (see Figure 31). These patterns of relations may suggest another layer of wolf social organization.

Wolf Social Organization

The analyses presented in this section have uncovered an interpack mating structure among YNP wolves. Mating alliances among packs were found and evidence was found for the existence of relations between alliances of wolves. Figure 33 is an illustration of wolf social structure as the analyses in this project suggests that it exists among wolves in YNP. The drawing in Figure 33 is inspired by the one Dunbar (1988:13) uses to demonstrate the layers of Gelada baboon social organization. As illustrated in Figure 33, wolves are members of packs, which form mating alliances.

Community refers to alliances that share structural relations. In the case of this project, two communities exist among YNP wolves. Potentially, there exist two communities among YNP wolves, as observable by the In-law relational (aqua-colored) ties in Figure 31. Community I exists among Alliances 1 and 4 (note the relation between the red and blue alliances), and Community II exists among Alliances 2 and 3 (note the relation between the green and gray alliances). There are also relational events that indicate coalition between alliances, as in the case of members of mating alliance 2 and 3 who in 2000 appear to be acting in a coalition against groups of domestic dogs owned by neighboring ranchers (see Figure 31).

The use of wolf "society" as a level of social organization refers to the set of wolves which interact with one another, presumably within some area that is bounded geographically, but not necessarily. In the case of this project, the wolf society contains the wolves reintroduced to YNP and their offspring.

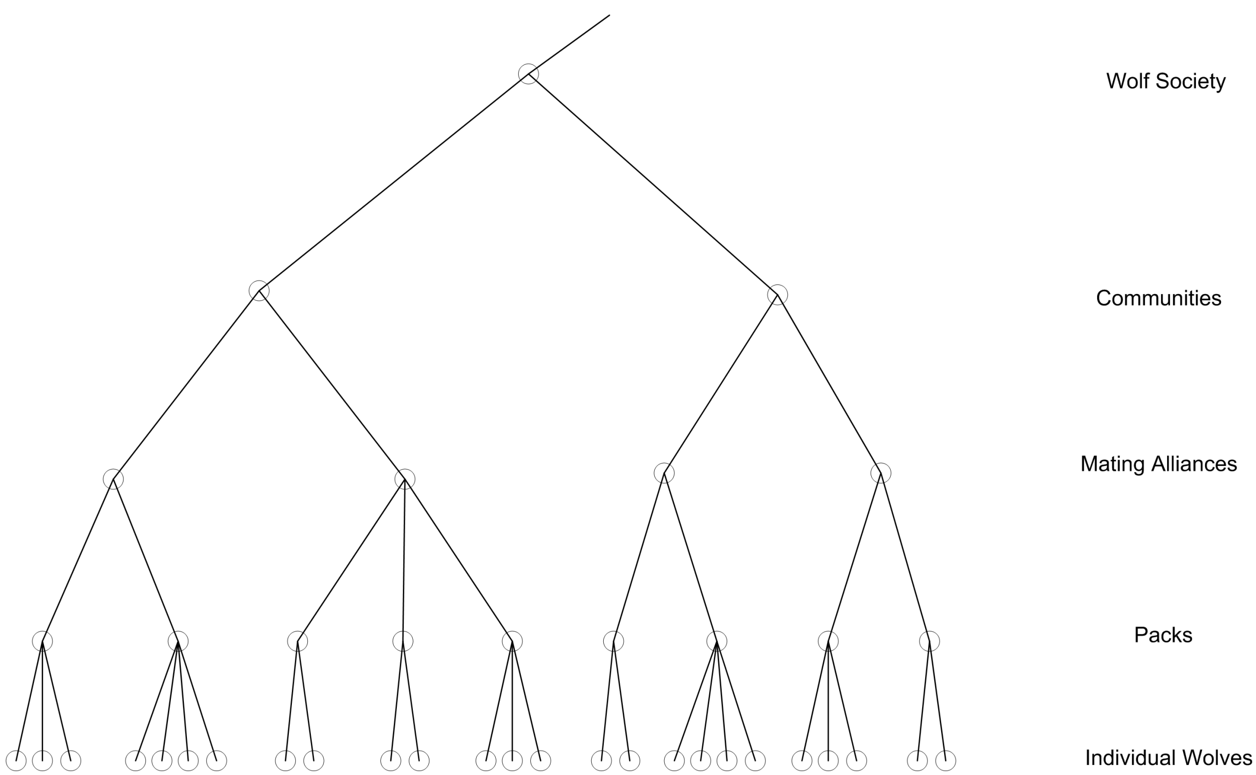

Figure 32: Layers of Wolf Social Organization

DISCUSSION

Interpack Relations

In previous research, pack was the only recognized unit of wolf social organization. That wolf packs form mating alliances with other wolf packs represents a dramatic departure from descriptions of wolf packs as isolated family groupings, which are generally hostile to outsiders. The longevity of packs, the formation of new wolf packs, and thus, to some extent the healthy survival of the species is dependent upon wolves pairing and reproducing with members from other packs of wolves. It seems unlikely that the only mechanism for interpack pairing is the meeting and mutual acceptance of two lone wolves. Clearly, interpack matings and the relational events described in this paper demonstrate that, at least for the wolves of Yellowstone National Park during the study period, non-hostile interpack interactions may be even more common than hostile ones, and that the mating structure appears to have some meaning for the actors. Although this study gives us some insight into "the occurrence of social tolerance in a population also demonstrating widespread intraspecific strife" (Mech et al. 1998), the mechanisms of social tolerance still remain a mystery.

Polygamous Mating

Finding such widespread polygamous mating activity was not anticipated. The literature indicates that wolf biologists have struggled with this aspect of mating behavior. While it has long been assumed that wolves are strictly monogamous animals (Mech 1970, Kleiman and Eisenberg 1973 and McDonald & Moehlman 1982 in Lehman 1993), it is more recently assumed that wolves are *mostly* monogamous animals (Mech 1999). However, repeated observations of polygamous mating practices among wolves (Zimen 1975; Harrington et al. 1982; Derix 1993) suggest that polygamy among wolves may be a commonly occurring form of wolf mating structure. Most interestingly, polyandry is considered the most frequently occurring form of polygamy among wolves (Zimen 1975; Harrington et al. 1982; Derix 1993). Among the wolf packs studied by Harrington et al. (1982), it is estimated that twenty-one (21%) to forty-one (41%) percent of those packs with more than one adult female are actually polygynous mating arrangements.

For the data used in these analyses, the Wolf Project's Annual Report implies that polygynous behavior among Yellowstone wolves may be due, in part, to the early stages of colonization. Smith et al. (2001:16) write, "Preliminary results suggested that immediately after reintroduction, Yellowstone wolves were more polygynous than in areas characterized by wolves in long standing populations." Findings from this project suggest a relationship between male's generation and mating behavior; Specfically, that polygynous mating arrangements are concentrated among the second generation of YNP male wolves. Also unusual are the instances of more than one breeding couple per pack in the year 2000. It seems we have much to learn about polygamous mating among wolves.

Yellowstone Wolves: A Special Case?

Ecologically speaking, Yellowstone National Park represents an environment that is extremely rich in resources for wolves. The phenomena studied in this project then are, at least to some extent, unique to wolves living under surplus conditions. The severe interpack aggression and territoriality (Mech 1970; Mech et al. 1998) observed among wolves in other wolf populations may be more common among wolves living under conditions where resources are more scarce. If this project were replicated using data generated from a wolf population living under conditions of scarcity, one might expect more interpack territoriality; and thus, fewer non-aggressive interactions between packs. Even in circumstances under which few new packs are forming, for the species to survive without inbreeding, wolves must secure mates from other packs. It is, therefore, logical to assume the existence of some interpack mating structure. Clearly, there is a great need for subsequent research in the area interpack social structure.

Recommendations and Implications for Future Research

This project is one among a small set of empirical investigations into the multi-layered nature of social organization among non-human social actors. Previous investigations of baboons (Dunbar 1984; 1988) and of dolphins (Connor et al. 1992) identified levels of organization based on cluster analyses of association data (actors observed interacting with or simply near one another.) Although studying primates, cetaceans, social carnivores and other non-human animals present differing challenges necessitating variety in methodological approaches, it may prove fruitful to apply to other animals some of the techniques and methods used in this social science investigation of mating alliances. Such investigations would not only generate new knowledge of (intergroup) alliance structure among the given subjects, but they would generate findings which could then be compared with existing techniques and potentially, stimulate a methodological discourse for the study of complex social organization among non-humans.

Ideally, one of the next steps for the study of wolf social organization would be the replication of this research using data generated by wolf populations living under differing sets of resource conditions. In addition, studying the kinship structure in a more established wolf population might prove especially insightful. Although longstanding populations do not allow for studying the emergence of social structure, the existing social structure can still be examined to determine if it has any meaning for the actors.

This paper has indicated that there may be levels of wolf social organization beyond the wolf pack. Further structural investigations of wolf populations which are modeled as closely as possible to the cluster analyses of dolphin (Connor et al. 1992) and baboon (Dunbar 1984;1988) association could serve as a good way to further explore structure beyond the wolf pack. Moreover, the relationship between these methods and the methods employed in this project could be explored.

Since findings from this project suggest that there is a relationship in Yellowstone between male's generation and mating behavior, re-examining this population based on these characteristics in subsequent years might prove fruitful. Also, since polygonous mating behavior may also be indicative of early stages of colonization in a wolf population, comparing the degree of polygamy in wolf populations at differing stages of colonization may be of merit.

A perspective that depicts the nature of wolf social organization as multi-layered is likely to generate research that provides new insights into wolf behavior. Moreover, certain wolf behaviors (such as interpack tolerance), which previously appeared puzzling to wolf researchers, might be better understood if they are considered within the context of interpack kinship relations. In addition, the existence of interpack relations that might have previously been unnoticed may become more apparent if non-hostile interpack behaviors are considered to be as plausible as hostile ones.

APPENDIX

Appendix A

Excerpt from the Wolf Narrative

January 1995: Fourteen wolves were captured from Alberta and brought to Yellowstone National Park. These wolves were numbered R2-R15. The wolves were placed in three, one-acre-sized enclosures in the northeast part of Yellowstone called the Lamar Valley for ten weeks. The three enclosures, and subsequently the first three reintroduced wolf packs, were called Rose Creek, Crystal Creek Bench and Soda Butte.

Table 13: Wolves Captured in Alberta and Released in Yellowstone Park in 1995

Pack	**Pack Location**	**Wolf**	**Age**	**Status**	**Original Pack**	**Weight (lbs.)**	**Release Date**	**Exit Date**
Crystal Creek								
		2M	**Pup**	**Sub**	**Petite Lake**	**77**	**3/21/95**	**3/31/95**
		3M	**Pup**	**Sub**	**Petite Lake**	**80**	**3/21/95**	**3/31/95**
		4M	**Adult**	**Alpha**	**Petite Lake**	**98**	**3/21/95**	**3/31/95**
		5F	**Adult**	**Alpha**	**Petite Lake**	**98**	**3/21/95**	**3/31/95**
		6M	**Pup**	**Sub**	**Petite Lake**	**75**	**3/21/95**	**3/31/95**
		8M	**Pup**	**Sub**	**Petite Lake**	**72**	**3/21/95**	**3/31/95**
Rose Creek		**7F**	**Pup**	**Sub**	**Mcleod**	**77**	**3/22/95**	**3/24/95**
		9F	**Adult**	**Alpha**	**Mcleod**	**98**	**3/22/95**	**3/29/95**
		10M	**Adult**	**Alpha**	**Rick's**	**122**	**3/22/95**	**3/29/95**
Soda Butte		**11F**	**Adult**	**Sub**	**Berland**	**92**	**3/27/95**	**3/29/95**

Table 13 (Continued): Wolves Captured in Alberta and Released in Yellowstone Park in 1995

12M	**Adult**	**Sub**	**Berland**	**112**	**3/27/95**	**3/29/95**
13M	**Adult**	**Alpha**	**Berland**	**113**	**3/27/95**	**3/29/95**
14F	**Adult**	**Alpha**	**Berland**	**89**	**3/27/95**	**3/27/95**
15M	**Pup**	**Sub**	**Berland**	**75**	**3/27/95**	**3/27/95**

While Penned (January, February, and March 1995)

Rose Creek Pack: R7F, R9F, and R10M

R7F and R9F arrived on January 12, 1995 (Smith in Phillips and Smith 1996).

R7F was the pup of R9F. R10M arrived on January 20th (Smith in Phillips and Smith 1996).

R9F and R10 mated in the winter of 95 (February).

“After a couple hours of growling, 9 and 10 did accept one another and they eventually mated in late winter.” (Ralph Maughan 1995-2001).

Crystal Creek Pack: R5F, R4M, R2M, R3M, R6M and R8M

All six wolves were captured from the same pack in Alberta and arrived on January 12, 1995 (Smith in Phillips and Smith 1996). Pups R2M, R3M, R6M and R8M are the sons of R4M and “are presumed to be” the sons of R5F (Ralph Maughan 1995-2001).

Rose Creek

Released on March 22nd (NPS Wolf Project Annual Report 1995-1996 1996, page 12). All three wolves exited through the open gate. R10M was the first to exit and “it was likely he did so fairly soon after we opened it” (Smith in Phillips and Smith 1996).

Two days after the gate was opened, on 3/24/95 researchers returned to the pen to cut a hole in the fence and left a deer carcass outside the pen as a lure. When they approached the pen, they heard howling from behind them and turned to find R10M standing about fifty yards behind them. The researchers abandoned the deer carcass and began to retreat. Dough Smith (in Phillips and Smith 1996, page 65),

> "We wanted to give #10 a wide berth, and not push him unnecessarily or move him away from the pen, because #9 was still in it. He was waiting for his mate to come out. Moving though the thick terrain on the bottom of the stream, we realized we were being followed. Wolf #10 was staying with us as we left the scene, howling as he went. … For twenty-five minutes, he followed us at a distance as we headed back. This was rare wolf behavior to be sure, but #10 was no ordinary wolf. Finally he left us, not willing to leave his mate, or follow us to more people."

"His (#10's) mate, female #9, did have trouble with the gate. It took #10 to lure her out, for he did not leave the pen until she joined him on the outside. That stormy day when he howled, he seemed to beckon her. But I have heard wolves howl like that before, and I was probably just reading more into it. Her pup, #7, probably followed the lead of the The Big Guy, exiting at about the same time as he, but she, too, waited for #9 on the outside until all three were untied before heading north". (Smith in Phillips and Smith 1996, page 70).

R9F exited the pen "around" March 29, 1995 (Phillips and Smith 1997:12).

"Upon release, [Rose Creek Pack members] #9F and #10M soon separated from yearling #7F (or perhaps it was the other way around)" (Maughan 1995-2001).

Rose Creek wolves #9F and #10M migrated "northward from the Park, over the very rugged and snowbound Beartooth Mountains, to a mountain (Mount Maurice) just above the town of Red Lodge, Montana" (Maughan 1995-2001).

April 24, 1995: #10M, Alpha male of the Rose Creek Pack and mate of #9F, was shot by "a local who was out bear hunting and had gotten his rig stuck in the mud" (Maughan 1995-2001).

April 24-26(?), 1995: #9F of the Rose Creek Pack gave birth to eight (8) pups on private land near the town Red Lodge, Montana. She had no pack members to help provide food for her and the pups. Yellowstone biologists captured #9 and her pups and placed them in the Rose Creek Pen (Maughan 1995-2001).

Spring-Summer of 1995: After her separation from her Rose Creek Packmates, "#7F remained in the Park, keeping to its northern portion, especially the expansive Blacktail Deer Plateau, which is a bit west of the territory that was claimed by the Crystal Creek Pack; and , after October, west of the territory of the newly invigorated Rose Creek Pack. She visited Gardiners Hole, the Mommoth Hot Springs area, and even Electric Peak in the Gallatin mountain range" (Maughan 1995-2001).

August 1995: A wind storm caused several fir trees to crash down on the Rose Creek Pen causing enough damage to the pen that #9F's pups escaped from the pen (Maughan 1995-2001). "Most (?) of the pups were recaptured and returned to the pen, but the rest remained nearby, were fed and kept out of trouble even though grizzly bears were beginning to show interest in the den area. The pups also became acquainted with wolf #8M, a sub-adult male from the Crystal Creek Pack" (Maughan 1995-2001).

Mid October, 1995: the yearling #8M dispersed from the Crystal Creek Pack and paired with #9F of the Rose Creek Pack. (Phillips and Smith 1996:13).

Mid October, 1995: Rose Creek #9F and her pups were released from the Rose Creek Pen. Yearling #8M of the Crystal Creek Pack, who had been hanging around the Rose Creek Pen area quickly joined #9F and her pups as the new Alpha male of the Rose Creek Pack. At this time, with 10 pack members, the Rose Creek Pack was the largest wolf pack in Yellowstone.

December 1995: #2M, who dispersed from the Crystal Creek Pack pairs with #7F, who dispersed from the Rose Creek Pack and the pair is dubbed "the Leopold Pack." "They were observed doublescent-marking and they have been seen together ever since. They keep almost entirely to the Blacktail Deer Plateau, where they are seldom seen" (Maughan 1995-2001). They settled on the Blacktail Deer Plateau establishing a territory of approximately 41 square miles (Phillips and Smith 1996:13).

April 1996: #7F Leopold Alpha female "gave birth to three pups" (Maughan 1995-2001).

May 1996: Rose Creek #9F "gave birth to three more pups at a den site on the lower Lamar River, about a mile upstream from its confluence with the Yellowstone" (Maughan 1995-2001).

Spring of 1996: #5F, Alpha female of the Crystal Creek Pack, "did den; but it is likely that the new and aggressive Druid Peak Pack killed her pups. The new Druid Peak pack did attack and kill her mate, #4M, and it appears that the Druids may have also injured her" (Maughan 1995-

2001). "#5F abandoned her den shortly after the Druids killed her mate, and she was seen limping with her tail held low for a while" (Maughan 1995-2001).

Middle of 1996: The Crystal Creek Pack is down to just 2 members, the Alpha female, #5F, and #6M (captured with #5F in Alberta) who is believed to be her son.

Winter of 1996-7: #9F Alpha female of the Rose Creek Pack mates with #8M Alpha male of the Rose Creek Pack (Maughan 1995-2001).

Winter of 1996-7: #18F, daughter and packmate of #9F, also mates with #8M (#18F's "step-father") of the Rose Creek Pack (Maughan 1995-2001).

April 1997: #9F, Alpha female of the Rose Creek Pack, denned "in full view of the NE entrance road" and bore seven pups. (Maughan 1995-2001).

April 1997: #18F, daughter and packmate of #9F, who also mated with #8M, digs "a more isolated [den] site under a rock near the Lamar River." She whelped eleven pups, but none of them survived "in part because of the location of her den" (Maughan 1995-2001).

April 1997: Rose Creek #19F, who remained with her pack, "denned, bore a litter from an unknown mate, but she was soon killed (probably by the nearby Druid Peak pack) and her [four] tiny pups soon died of malnutrition and exposure" (Maughan 1995-2001).

Mid May 1997: #9F of the Rose Creek pack "moved her den to a less visible location" (Maughan 1995-2001).

December 1997: 18F is the only one of the 1995 pups who remained with the Rose Creek Pack (Maughan 1995-2001).

April 1998: Rose Creek females, #9F and her daughter #18F denned together. "They jointly produced eleven more pups. It is not possible to say which pups belong to which mother" (Maughan 1995-2001).

April 1999: "#9F and her daughter 18F, denned again (the 5th year for #9F and the 3rd year for #18F). In 1999 they denned separately (as they had done in 1997), but later they joined their litters and moved up with most of the rest of the pack to their tradtitional summer range on the roadless Buffalo Plateau" (Maughan 1995-2001).

April 1999: The Leopold Pack's alpha female, "#7F whelped her 4th litter of pups. Four pups have been counted in this rarely seen pack which, ironically [?], inhabits the Blacktail Deer Plateau just north of the Mammoth to Tower Jct. Road" (Maughan 1995-2001).

September 1999: "Beginning in September, matriarch #9F of the Rose Creek Pack was seen less and less frequently together with her vast pack, number perhaps 30 members. Now she is missing, but appearently not dead because radio collars give out mortality signals. I means she is probably out of the normal tracking flight range. A special flight will made to try and locate her" (Maughan 1995-2001).

Mid February 2000: "Number 9 was gradually pushed away from Rose Creek pack last fall, presumably by her daughter, born to her and the then-late alpha male 10M in April 1995. At the age of 8 or 9 years, no. 9's black coat has turned silvery gray; and some thought she was doomed to live her remaining, likely short life, living on the outskirts of other wolf packs. The surprise is that she is with three other wolves. Two of them are black males. The other, a female, is from her old Rose Creek Pack. The pack was discovered on Valentine's Day and will be named the Valentine Pack. It's range appears to be the headwaters of the Clark's Fork of the Yellowstone, just SE and over the "hill" from Cooke City, Montana. My experience in the area indicates there are a lot of elk, deer and moose to eat. There are also some cattle, horses, livestock dogs, and pet dogs in the area. In fact one pet dog was killed in the area by a wolf just a month or so ago." (Maughan 1995-2001).

March 8, 2000: "Valentine Pack. The pack is east by northeast of Yellowstone. Apparently this is not yet the official name of this newly discovered pack, of which 9F is probably the alpha female. The pack has 4 adult wolves, 2 males and 2 female. The second female, 153F (born in 1998), is from the Rose Creek Pack, and is possibly one of 9's daughters. Three of the wolves are black. No. 9 is now silvery gray. Of the two male wolves, the smaller male seems to be dominant. The larger male, 164M, is known to be a disperser from the Sheep Mountain Pack, north of Yellowstone. The Valentine Pack may have pushed the larger Sunlight Basin Pack a bit southward. The larger Sunlight Basin Pack has only two adult wolves. The rest are pups" (Maughan 1995-2001).

April 4-14th: "April 4 and 14, 2000. Valentine Pack- It was reported today that no. 9 does not appear to be the dominant female in the new Valentine Pack, NE of Yellowstone. Recent observations of the new pack, based on wolf body language, indicate that no. 153F (9's daughter) appears dominant. Whether one or both females in the pack are pregnant should soon be known because denning time is about to arrive. Not all biologists agree that no. 9 has been displaced" (Maughan 1995-2001).

July 5, 2000: "The biggest is the presumed natural mortality of the alpha male (8M) of the Rose Creek Pack. He was found by Doug Smith yesterday pinned under a log, underwater in Slough Creek. The cause of his death was not readily apparent, but it is probably natural (perhaps a soft tissue injury from his potential prey).

No. 8M was, of course, the second mate of famous no. 9F. Born six years ago, no. 8 was just a youngster from the nearby Crystal Creek Pack when no. 9 and her 8 pups were re-released from the Rose Creek Pen in the fall of 1995 (her original mate, no. 10M was illegally gunned down by Chad McKittrick in April 1995). No. 8 discovered the penned wolves; and he stayed nearby until they were released, and the big Rose Creek Pack formed almost immediately.

No. 8 and 9 were the alpha pair of Rose Creek until last fall, when no. 9 was driven from the pack (she is still alive and may have a new litter of pups east of the Park). No. 18F (her daughter born in 1995) is the present alpha female and was observed yesterday with 5 pups.

Another venerable alpha, no. 5F, long time leader of the Crystal Creek Pack, seems to have left the pack. She was another of the original 1995 wolves. Over the last 8 months a number of alphas have died, been killed or have left their packs: no. 5F (Crystal), no. 8M (Rose Creek), no. 9F (Rose Creek), no. 14F (Soda Butte), and no. 40F (Druid Peak)" (Maughan 1995-2001).

July 19, 2000: "Final necropsy report was that no. 8 suffered a natural death of unknown causes" (Maughan 1995-2001).

July 21, 2000: "The wolves of Wyoming outside Yellowstone Park are faring well, most have new pups, and they are avoiding cattle.

There are now probably three packs of wolves in the Sunlight Basin area, or more generally the mountain region between the NE side of Yellowstone and the plains at Cody, Wyoming.

There is the Sunlight Pack, which now has its second litter of pups, four black ones. There is also the new Absaroka Pack, consisting of 153F and 164M, plus another uncollared adult wolf. They have five pups.

Number 9F denned, and she has an uncollared companion. Mike Jimenez recently examined her den site and found no pups, but then she would have moved them to a rendezvous site by now anyway. No. 9, the former alpha female of the Rose Creek Pack, will be the alpha of what will be called "the Beartooth Pack" if she and her companion have pups An article today in the *Billings Gazette* by Michael Milstein indicates the wolves are passing through cattle on their way to hunt deer and elk, and have not harmed the cattle. . . so far an ideal situation. Number 9, of course, lived in Yellowstone for years and it unlikely to consider livestock to be prey." (Maughan 1995-2001).

August 17, 2000: “The Rose Creek Pack is in its usual haunts. The females with pups appear to be 18F and 156F. 156F just dropped her radio collar”. (Maughan 1995-2001)

August 17, 2000: “Famous wolf number 9F unfortunately got her first taste of cattle flesh due to a depredation by a grizzly bear. Here is the story as written by the U.S. Fish and Wildlife Service.

‘. . . a freshly killed cow was located near the old #9 den site and #9 was nearby. The carcass was being fed on by a female grizzly with 2 cubs. As the plane circled the bear became nervous and moved away from the carcass, and #9 rushed in to feed. The bear then rushed back to defend the carcass. This went on for several minutes but finally the bear moved off (probably because it was the animal most disturbed by the circling aircraft) and #9 claimed the carcass. WS investigation indicated it was a confirmed grizzly kill, but this does indicate that a host of scavengers and predators are in competition for carrion and kills. A similar situation occurred on an allotment near the Gros Ventre pack rendezvous site, which confirmed grizzly kills were usually also visited by wolves. The reverse has also been documented. Grizzly bears commonly take wolf kills away from entire packs. This situation complicates identification of the cause of livestock losses and emphasizes the need for quickly finding and investigating carcasses to accurately determine cause of death’” (Maughan 1995-2001).

August 23, 2000: “The wolves of Wyoming outside Yellowstone Park are still faring well. It is still not known if no. 9 has pups, and other wolves have had been a few run-ins with dogs and one calf” (Maughan 1995-2001).

August 23, 2000: "Number 9F denned, and she has an uncollared companion. She moved her den once, and while no pups have been seen, she would be unlikely to dig a second den if there were no pups. Her range is mostly in thick timber and she is hard to observe. There is no official call on whether she has pups yet. Many people have asked me. Her pack is named the Beartooth Pack, or if no pups the Beartooth Pair**.** Number 9 recently tasted her first beef when she sampled a cow killed by a grizzly bear. The bear reclaimed the kill, but was scared off by the search plane" (Maughan 1995-2001).

September 17, 2000: "The Rose Creek Pack is in its normal territory, but spread out with all four radio-collared members of the pack located in different areas" (Maughan 1995-2001).

September 17, 2000: "Number 5F is still apart from her former pack, wandering alone, but apparently in good condition. The rest of the Crystal Pack is in the Pelican Valley and has observed in many interactions with grizzly bears this summer. Of course, the Pelican is 'grizzly central'" (Maughan 1995-2001).

September 17, 2000: "The new Absaroka Pack east of the Park fares well with its 3 adults and first litter of pups. It is still not known if famous no. 9F and her companion of the Beartooth Pack/pair has pups due to the dense timber of the area. I would say circumstantial evidence is that they have one pup or more (based on her travel and hunting patterns)".

October 17, 2000: The Rose Creek Pack may be splitting. Pack member 190M and two other pack members were seen on an elk kill far south of the main body of the pack which was north of the Park in the headwaters of Slough Creek. The most interesting observation was that wolf 150M, a disperser from the Leopold Pack may be Rose Creek's new alpha male. The old alpha no. 8M was found dead this summer of presumed natural causes in Slough Creek" (Maughan 1995-2001).

November 2, 2000: "Several folks have contacted me with the story that Yellowstone wolf no. 5F, former alpha female of the Crystal Creek Pack, was seen on the morning of Nov. 2 feeding on an elk carcass with a number of the now greatly enlarged Druid Peak Pack. Nos. 4M and 5F were the original alpha pair of the Crystal Creek Pack, brought from Alberta to the Park in the late winter of 1995. A number of their pack mates were brought with them and they were released from the pen on Crystal Creek Bench in March 1995. The Crystal Creek Pack dominated the Lamar Valley in 1995 and early 1996. During that time, however, two of their pack dispersed. One became the alpha male of the Rose Creek pack (8M), and the other the alpha male of the new Leopold Pack (2M). Number 3M was shot north of the Park by Wildlife Services after killing some sheep. That left the pack with just three members 4M, 5F, and what was thought to be their son, 6M. In May 1996 the alpha male (4M) of the Crystal Creek pack was killed by the new Druid Peak Pack. The Druids may have also injured 5F and killed her litter of pups (that she had pups is speculation). Story 5-22-96: YNP Mortality: Crystal Cr. alpha male. 5F and 6M then left the Lamar and drifted south to the Pelican Valley and eventually formed what became the large rejuvenated Crystal Creek Pack. No. 6M continued to grow and may have become the biggest wolf in Yellowstone. In early 1998 he was trapped for re-radio-collaring and weighed 141 pounds! The also became the first pack to kill bison, and they continue to do so today. Nevertheless, 6M was killed in late August 1998, probably by an elk that was found dead of wolf attack nearby. It is also possible a grizzly bear killed him. Story (9-1-98): Crystal Creek Alpha male died in natural mortality. Still the pack prospered, but last fall it was discovered the 5M was no longer its alpha female; and because the pack had no pups in 2000 and many members had dispersed, it seems to be a pack on the decline. Nevertheless, the remaining members of the pack all seem to be notable for their large size. There is irony that no. 5 has now been observed with her arch-enemy the Druid Peak Pack, but that pack too is now much different, with only the present alpha female, no. 42F, having any possible memory of the events of May 1996. " (Maughan 1995-2001)

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