

Group composition effects on inter-pack aggressive interactions of gray wolves in
Yellowstone National Park

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ABSTRACT

Gray wolves (*Canis lupus*) are group-living carnivores that defend group territories and direct aggression against conspecifics. Here, I document 292 inter-pack aggressive interactions during 16 years of observation in Yellowstone National Park (YNP). I recorded pack sizes, compositions, and spatial orientations related to residency to determine their effects on the outcomes of aggressive interactions between groups. This represents the first attempt at directly observing aggressive interactions over an extended period and subsequently using pack characteristics to determine which groups had an advantage over their opponents. Relative pack size (RPS) was the most important factor in the odds of a pack being able to successfully displace their opponent. However, when RPS was fixed, packs with more old (>6.0 years old) members or with more adult males also had higher odds of winning. I discuss these results with respect to the adaptive value of sociality and the relative importance of certain individuals during inter-group interactions. While the importance of RPS in successful resource- and territory-defense suggests the evolution and maintenance of group-living may be due to larger packs' success during inter-pack interactions, group composition—which can change irrespective of group size—is also an important factor highlighting that some individuals are more valuable than others during inter-pack conflicts.

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INTRODUCTION

Many gregarious mammals aggressively defend group territories (Table 1-1). Among carnivores, group members often use vocalizations and scent-marks to denote territory boundaries (gray wolves [*Canis lupus*] Peters and Mech 1975; coyotes [*Canis latrans*] Barrette and Messier 1980; golden jackals [*Canis aureus*] Jaeger et al. 1996; Ethiopian wolves [*Canis simensis*] Sillero-Zubiri 1998; spotted hyenas [*Crocuta crocuta*] Boydston et al. 2001, Benson-Amram et al. 2011). They also direct aggression against alien or neighboring conspecific groups or individuals (Table 1-1). Territorial defense allows these groups to monopolize their own resources such as food, mates, and space and prevent their competitors from access to them.

Intergroup interactions can result in injuries and fatalities to individuals (e.g., gray wolves Mech 1994, Mech et al. 1998; African lions [*Panthera leo*] Mosser and Packer 2009) and can result in long-term effects on both groups involved in the interaction (chimpanzees [*Pan troglodytes*] Mitani et al. 2010; gray wolves Yellowstone Wolf Project, unpublished data). The loss of adult group members may reduce the competitive strength of the group (Wrangham 1999), and failure to defend against intruders may result in the loss of resources, territory, and the lives of group members. This may eventually lead to group dissolution (e.g., chimpanzees Goodall 1986, African lions Packer et al. 1988; gray wolves Mech et al. 1998, Yellowstone Wolf Project, unpublished data).

Although gray wolves have been extensively studied (Mech and Boitani 2003), little is known about inter-pack interactions and aggression. Direct observations of

interactions are rare and only a few anecdotal accounts have been described (Murie 1944; Marhenke 1971; Mech 1966, 1993; Mech and Frenzel 1971; Mech et al. 1998). These interactions often include the chasing and sometimes killing of rival wolves (Mech and Boitani 2003), and most have been found to take place within a buffer zone between pack territories (Mech 1994).

Although territoriality is an underlying theme in many studies of group-living species, a mechanistic understanding of territoriality and intraspecific aggression still represents an important gap in the current knowledge. Wolves are territorial (Mech and Boitani 2003), but very little is known about how inter-pack interactions and aggressive territorial defense are affected by pack compositions and demographics.

In this study, I examine the effects of pack composition on the outcomes of aggressive intergroup interactions between gray wolf packs using 16 years of individual-based behavioral observations following the gray wolf reintroduction to Yellowstone National Park (YNP), Wyoming (Bangs and Fritts 1996; Smith and Bangs 2009). The presence of several possible prey species and wide, open valleys for unhindered observation combined with a large number of radio-collared and individually-recognizable wolves make this area ideal for observing rare behavioral episodes. During the data-collection period various biologists, technicians, and I witnessed and documented 292 intergroup interactions. In nearly every case we were able to determine outcome and the role of individual pack members and to catalog their level of participation. We recorded several types of interactions (see Methods section for classification rules); but only interactions between packs were used for this analysis. I

posit that pack-pack interactions provide the best data to examine two groups contesting resources.

Here I use multivariate, mixed-effects models and backward stepwise selection to determine the influence of group characteristics and composition on success during intergroup aggressive interactions. Based on intergroup-aggression studies in other social mammals (e.g., coyotes Gese 2001; African lions Mosser and Packer 2009), I predicted that groups would be more likely to win if they (1) outnumbered their opponent, (2) were residents, and (3) included relatively higher numbers of individuals more likely to be aggressive—(i.e. adult males, prime-aged adults, and breeders). I discuss the implications of my results with respect to the adaptive value of sociality. Specifically, that evolution and maintenance of group-living may be driven by larger groups' superior ability to protect themselves and their resources during inter-group aggressive interactions. Knowledge of characteristics that promote group success during intraspecific encounters is key to understanding the adaptive advantages of sociality for many species, including humans, and also how some individuals in a group may be more valuable than others, a relatively neglected idea in research on social animals.

STUDY SYSTEM

We collected all data on the Northern Range (1,000 km² [Appendix A]) of YNP (8,991 km²). The Northern Range is defined by the seasonal movements of the elk (*Cervus elaphus*) in the area. Elevations there vary from 1,500 to 2,400 m, with high elevations characterized by conifer forests and low elevations by open grass meadows and shrub-

steppe vegetation (Houston 1982). The area experiences long, cold winters and short, cool summers (Dirks and Martner 1982) and features a high wolf density fluctuating between 20 and 98 wolves/1,000 km² with an average of 56 (Smith et al. 2011).

Although elk are the wolves' primary prey in the area (Smith et al. 2004; Fortin et al. 2005; Metz et al. 2011), other prey residing on the Northern Range include mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americanus*), bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and mountain goat (*Oreamnos americanus*). Other common predators include black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), mountain lions (*Puma concolor*), and coyotes (*Canis latrans*). Areas within YNP are protected from consumptive human activities such as development, hunting, and livestock grazing.

METHODS

Telemetry collars

As part of its long-term research, the Yellowstone Wolf Project captures 15-30 wolves each year via aerial darting. Biologists fit wolves with standard Very High Frequency radio collars (Telonics, Inc. Mesa, AZ) or Global Positioning System radio collars (Smith and Bangs 2009) and track them aerially once a week and from the ground opportunistically, except during the biannual winter studies from March 1 to 30 and from November 15 to December 14 when they track packs daily. The National Park Service approved all capture and handling protocols and confirmed they were in accordance with recommendations from the American Society of Mammalogists (Sikes et al. 2011).

Data collection

Trained observers (including myself) usually recorded wolf behavior from 0600 to 1000 and 1500 to 1900 hours by driving park roads radio-tracking collared individuals. When we detected a signal, we searched for the pack or individual using spotting scopes, and observed the packs most often from distances of 0.25 to 6.00 kilometers. Upon locating a pack we recorded the individuals present, because pack members were not together all the time.

During routine tracking, if we located two packs or a pack and a lone wolf within a few kilometers of each other we considered that an intergroup interaction may be imminent. We selected a nearby observation point from which we could record the composition and behavior of both groups. If the groups travelled away from each other or an encounter seemed otherwise less likely, we did not record an interaction. Because intergroup interactions occurred infrequently and unpredictably, we recorded interactions ad libitum (Altmann 1974) and observed them only on the Northern Range where we could make year-round observations.

We recorded the locations of all interactions by reference to landmarks using USGS maps (1986) and plotted precise points using Universal Transverse Mercator (UTM) grids. We classified locations of both packs as to whether they were resident, intruder, or in territory overlap by examining the interaction locations in relation to the packs' 95% Minimum Convex Polygon (MCP) for the current year. If the interaction occurred within 95% MCP, the pack was listed as resident unless another pack's 95%

MCP overlapped the locations, whereas they were classified as in territory overlap. Packs were classified as intruders if the interaction occurred outside their 95% MCP boundary.

For each intergroup interaction, we recorded: (1) age, sex, and breeding status compositions of both groups, (2) time observation began, (3) time it ended, (4) which group initiated interaction, (5) the locations of both groups at the beginning and the end of the interaction, (6) the behavior of all individuals in each group related to initiation and participation in the chase, attack, kill, or flee events, and (7) the results of the interaction: win or loss.

I omitted interactions based on the following criteria: (1) terrain or weather made it impossible to observe interactions (n = 8), (2) confusion over identification (n = 5), (3) the interaction was likely intra-pack (n = 8), or the interaction was compromised by a single wolf under the effects of capture drugs (n = 1).

Individual characteristics. - We recorded individuals' sex, age (date of birth), and weight during the capture and radio-collaring process. We made significant effort to observe breeding behavior and distinguished an individual as a breeder if we observed it in a copulatory tie or actively trying to copulate during the current year's breeding season. We also used genetic analysis to determine breeding status if results confirmed at least one offspring was sampled (vonHoldt et al. 2008; Stahler et al. 2013). We used year-round observations to determine the sex, age, and breeding status of uncollared individuals. After repeated observations, many uncollared wolves were individually-recognizable based on body morphology, pelage coloration, injuries (e.g., permanent limp, tip of tail or ear missing), and hair loss patterns due to mange.

We used urination posture to determine sex of unmarked individuals. Males performed STU- standing urinations or RLU- raised leg urinations, whereas females performed SQU- squat urinations or FLU- flexed leg urinations (Peters and Mech 1975).

We determined ages for captured wolves most easily when we captured them as pups. We used tooth wear on live individuals and cementum annuli measurements on dead individuals to determine their birth year (Gipson et al. 2000). We considered wolves captured as adults to be known-aged if individually recognized as pups due to some morphological features (e.g., pelage marking, color, body shape, and size). I used continuous ages to assign individuals to age categories (i.e. pups less than 1-year old, yearlings between 1 and 1.99, prime-aged adults between 2 and 5.99, and old adults more than 6-years old (MacNulty et al. 2009b; Stahler et al. 2013).

We dictated observations of intraspecific interactions on portable voice recorders and later completed data forms. In 81% of observed interactions multiple observers witnessed the same interaction. Observers recorded separate notes and collaborated to complete a single, unified account of each interaction. Our observation effort changed throughout the year as six to nine observers took part in the biannual Winter Studies (March and November-December) instead of the usual two to three year-round observers. Although many technicians (n = 27) contributed their observational data to this study, the five technicians with the longest terms recorded 71% (208 interactions) of the total. I observed and recorded 12% of the total interactions, the second- most of all observers.

Videographer Bob Landis recorded several aggressive interactions. I used these videos to verify the accuracy of data obtained solely from transcribed notes. Using 14 video-recorded interactions, I found that audio-transcribed notes were an effective

method of recording inter-pack interactions. Although recording less detail, observers using dictaphones still obtained accurate data on the major events and participants in an interaction. In recording the numbers and identities of the wolves present during an interaction, as well as which pack chased, attacked, killed, howled, and/or fled, observers correctly filled out 94% of the questions on the data form.

Intergroup interactions.- I determined an interaction occurred when at least one wolf had auditory (howling) or visual contact (looking in the direction of opponent and reacting either by subsequently running away, charging forward, or following opponent's movements with eyes) with a lone wolf or at least one wolf from a different pack. We recorded all events during an interaction: howl, approach, watch, chase, attack, kill, stand ground, flee, or socialize. An interaction was aggressive if it included a chase which was when at least one wolf ran toward at least one opposing wolf and that wolf fled. Occasionally wolves or packs ran toward each other and fought before one pack or individual fled. In such cases a chase was always accompanied by a wolf eventually fleeing. Interactions escalated to an *attack* if at least two opponents made contact (usually biting) and to a *kill* if an individual was attacked and killed or fatally wounded.

I classified aggressive interactions based on both groups' sizes. When two packs of two or more individuals interacted I considered it a pack-pack interaction, when a pack interacted with a single, non-pack member—a pack-individual interaction, and when two single individuals from different packs interacted—an individual-individual interaction. For this study we always used the term "pack" when describing a group of wolves, even if some pack members were missing at the time of an interaction. During recorded

interactions, packs contained all members 58% of the time and otherwise were usually missing <25% of the pack members.

Interaction outcome. -For pack-pack interactions, I assigned a WIN to the group that displaced the other or caused it to flee and assigned the fleeing group a LOSS. An intergroup interaction ended when all participating individuals stopped showing signs of chasing or fleeing, usually by lying down to rest.

Collared wolf mortalities.-When collared wolves were found dead we performed necropsies as soon as possible to determine cause of death. We confirmed a wolf had been killed by other wolves when it had hemorrhaging caused by puncture wounds of the appropriate size for a wolf (approximately 35-55mm between canines) and focused bite-wounds to areas typical of wolf attacks: head, neck, groin, and flanks. We took note of other packs in the area of the mortality to determine the possible attackers.

DATA ANALYSIS

To understand the influence of pack characteristics and composition on aggressive territorial defense, I examined their effects on successful and unsuccessful intergroup interactions. Our analyses used generalized linear mixed models (GLMMs) with a binomial distribution, resulting in logistic regression models. To account for unmeasured, idiosyncratic variables associated with certain packs, and repeated measures of some packs, I used the pack (PACK_ID) as a random variable in all models.

I examined only those interactions that were observed to determine a winner and a loser based on which pack displaced the other and randomly chose one side of the pack-pack interactions ($n = 121$) for analysis to eliminate dependence between opponents. I used the other half of the data to verify reported trends and influences. I did not analyze pack-individual and individual-individual interactions with respect to wins and losses, because they were more likely to include nonaggressive interactions between the individual and some pack members as the loners tried to join packs or breed with their members.

I used relative pack size (RPS—e.g., if packs with 5 and 7 members interact they are assigned RPS scores of -2 and 2, respectively) and so assigned opponents of equal size zeros instead of total (numerical) pack size to capture the pack's size in relation to their opponent. I predicted RPS would have a strong influence on interaction outcome as a numerical advantage in other species often allows a larger group to defeat a smaller group (coyotes Beckoff and Wells 1986; chimpanzees Manson and Wrangham 1991; Wilson and Wrangham 2003).

I predicted that the location of the interaction with respect to each group's territory could be an important variable as residents of many species are more likely to win over intruders (Davies 1978; Cheney 1981; Maynard Smith 1982), because residents either (1) are better at fighting and therefore accumulate in the best territory, (2) have more to gain from their territory—such as knowing the best places to hide or feed, or (3) don't necessarily win except those times decided by some arbitrary convention (e.g., whoever gets to the area first, wins; for details, see Krebs 1982).

Behavioral differences between males and females during intergroup interactions (spotted hyenas Boydston et al. 2001; common marmosets [*Callithrix jacchus*] Lazaro-Perea 2001; chimpanzees Wilson et al. 2001, 2012) suggest that groups having a numerical advantage of the more aggressive sex may be more likely to defeat their opponents. I predicted that packs with more adult males would be more likely to win, because males are the more aggressive sex (Yellowstone Wolf Project, unpublished data)—similar to other species—(e.g., common marmosets Lazaro-Perea 2001; chimpanzees Wilson 2001, Wilson et al. 2012; and olive baboons [*Papio anubis*] MacCormick 2012), and their aggressiveness increases with age (Yellowstone Wolf Project, unpublished data).

I predicted that prime-aged individuals—those at their peak physical abilities—would be those most likely to escalate (initiate or participate in chasing, attacking, or killing opponents) during an interaction (much like free-ranging dogs [*Canis familiaris*] Pal et al. 1998; and Japanese macaques [*Macaca fuscata*] Majolo et al. 2005), and similar to gray wolf hunting behavior (MacNulty et al. 2009b). Although this aspect has been little studied in other species, I predicted packs with more breeders would have more incentive (the addition of mate defense to territorial defense) to escalate during an interaction (e.g., guerezas [*Colobus guereza*] Fashing 2001; banded mongoose [*Mungos mungo*] Cant et al. 2002). Consequently, groups with more prime-aged individuals and breeders would be more likely to win. My examination of group dynamics during intergroup interactions where one group is successful and the other is not should provide powerful insight into the mechanisms behind group-living and territoriality.

Prior to testing models, I examined each of the variables for correlation. Because some of the variables were highly correlated ($r > 0.70$) with RPS (Table 1-2), I removed them from further analysis (relative number of males, females, pups, blacks, and non-breeders). I then tested the relative importance of some related variables (e.g., age categories, as in the number of yearlings, prime-aged adults, and old adults) and also tested their importance when controlling for RPS (Table 1-3).

I started with a saturated mixed-effects, logistic regression model and used backward stepwise selection to determine the best reduced model for predicting a successful interaction based on my variables. I dropped non-significant variables ($p < 0.05$) one at a time until a likelihood-ratio test indicated that the fit of the reduced model was significantly worse than that of the previous model containing the dropped variable. Once I reached a reduced model I refitted the omitted variables one at a time and tested for significance. I also tested for interactions between variables in the best-fit model by adding interaction terms to the model one at a time and testing for significance. I calculated fitted values from the best fit model with marginal expectations of the three variables averaged over the random effect of pack ID and conditional on the observed variables. I used Stata12 for all analyses and report means with standard errors (SE).

There were many times two packs interacted out of sight or during the night and we only tallied these interactions with certainty if a collared wolf was killed ($n = 43$). I did not use this data in the analysis of model selection but only used it to compare to the model selection results. I was often able to deduce the pack responsible for the death of a rival wolf and assigned a level of certainty to the attackers (i.e. *definite* if the attackers were located in the immediate vicinity [≤ 1 km] of the fresh collared wolf carcass or GPS

collar locations put attackers at the kill location, *probable* if the attackers were located within 15 km of the carcass and there was evidence of an interaction [e.g., bark-howling, one pack split up and trying to regroup, an ungulate kill made by one pack and taken over by attacking pack], *possible* if the attackers were located within 15 km of the carcass with no other known packs in the area, and *unknown* if the carcass of the wolf was well within its own territory and there was no evidence of other packs in the area, in areas where we had no knowledge of neighboring packs, or two or more packs were nearby and the identity of the attackers could plausibly be either pack). I only included wolves killed by other wolves if the attackers were known with *definite*, *probable*, or *possible* certainty. Several wolves were likely killed by members of their own pack ($n = 3$), and I did not include them in this examination of intergroup aggression. I tabulated the typical pack size of the two packs (the pack experiencing a mortality and the attackers) to see if the relationship between RPS and mortality events was similar to RPS and observed success or failure during an interaction.

RESULTS

During >5,300 observation days, we recorded 292 intergroup interactions involving 33 different packs for analysis: 121 pack-pack (41.4%), 166 pack-individual (56.9%), and five individual-individual interactions (1.7%) (Appendix B). Interactions varied in intensity level reached. One hundred percent of aggressive interactions reached a chase, while 71 (24.3%) escalated to a physical attack, and 12 (4.1%) resulted in a fatality.

Most interactions occurred during February (48 [20.1% of the total interactions]), December (41 [17.0%], and January (33 [13.8%]), the months preceding the breeding season in mid to late February. Few aggressive interactions occurred during summer—June through September (5-9 [2.1-3.8%]) [Figure 1-1]. This result was corrected for uneven observation effort during the biannual winter study months. November and December interactions were divided by 1.5, because both had 180 hours of observation more than the average of 360 observation hours per 30 days. March was divided by 2, because it had twice as many (720 h) observation hours compared to the remaining nine months.

Effects of group composition.—In a model testing the influence of three age classes (yearlings, prime-aged, and old; relative number of pups was not included, because it was highly correlated with RPS) on winning an interaction resulted in all three categories being significant until RPS was included in the model, then only the relative number of old individuals was significant (Table 1-3; Models A & B). When I combined those three age categories into “adult” and divided them into males and females, both variables “relative number of adult males” and “relative number of adult females” were significant until RPS was added to the model, and only relative adult males remained significant (Table 1-3; Models C & D). Variables used for model analysis are listed in Table 1-4.

Effects of group size.—Winning packs often had RPS values of more than zero and losing packs less than zero (Figure 1-2). In addition, packs with RPS of < 0 experienced more intraspecific mortalities (Figure 1-3). Because we estimated pack size in this part of

the analysis (as opposed to having a known pack size for observed interactions) there are some cases where a pack with an estimated $RPS > 0$ lost an individual. This may be a true reflection of the interaction, it may be that the pack that experienced the mortality did not have all members present, or had relatively higher numbers of the most valuable individuals (see Model Selection section below). In addition, packs with $RPS < 0$ may also have some pack members missing and the estimates should be considered maximums. Regardless, these results support the behavioral data results suggesting that small differences in relative pack size had a significant effect on success. Further, most packs experiencing a mortality had $RPS > -5$ and < 0 , indicating that packs only slightly smaller than their opponent lose more members than those much smaller (< -5) than their opponent. These results may indicate packs of similar size create a hyper-competitive environment or that smaller packs are successful at avoiding aggressive interactions.

Model selection. – Backward stepwise selection results suggested that the combined effects of RPS, relative number of old pack members, and relative number of adult males had the most influence on success during intergroup interactions (Table 1-5). The main effect for RPS suggests packs that are larger than their opponents are more likely to win. Specifically, the odds ratio of RPS is 2.4, meaning the odds of winning increased by 140% ($[\text{odds ratio score} - 1.00] \times 100 = \% \text{ change in odds of winning}$) with one additional wolf. Because each additional wolf builds on the previous RPS's compounded rate, adding three wolves means the odds of winning ($2.4^3 = 13.82$) for a pack with $RPS=3$ was nearly 14 times greater than for a pack with $RPS = 0$.

The relative number of old individuals was also included in the best reduced model. The odds ratio for this variable was 2.5 and indicated the addition of one old wolf increased a pack's odds of winning by 150%. The chances of winning an interaction also increased when the relative number of adult males increased; the addition of one relative adult male (odds ratio = 1.65) increased a pack's odds of winning by 65%. I used the best-fit model to predict values for all three terms by calculating the fitted values—while holding the other two terms fixed (Figure 1-4).

DISCUSSION

Understanding the evolution of group territorial defense requires knowledge of the behavioral components of direct interactions and what characteristics of each group determine the outcome. Our study is the first to offer insight into the mechanics and proximate results of intergroup aggressive interactions among gray wolves when the interactions and pack dynamics are directly observed. Most previous studies on intergroup interactions were forced to use collared wolf mortalities in combination with tracks and disturbed vegetation or snow to make inferences about the results (Mech 1977, 1994; Mech et al. 1998; Peterson et al. 1998). Our results indicate that pack size, number of old adults, and number of adult males are key factors in a pack's ability to win an interaction.

Relative pack size. –Numerical advantages leading to successful intergroup interactions are well documented in other species (African lions, Packer et al. 1990; chimpanzees,

Wilson et al. 2001, 2012; spotted hyenas, Benson-Amram et al. 2011) and our work supports these findings. The importance of a numerical advantage in successfully defeating an opponent suggests that territorial defense is an important driver in the evolution and maintenance of group-living among territorial mammals. While other studies have come to this same conclusion (e.g., African lions Mosser and Packer 2009), several other explanations for sociality have been proposed.

Particularly among carnivores, researchers hypothesize that sociality provides hunting (spotted hyenas Kruuk 1972; African lions Schaller 1972; African wild dogs [*Lycaon pictus*] Creel & Creel 1995; gray wolves MacNulty et al. 2012), foraging (gray wolves Thurber and Peterson 1993), and survival (gray wolves Smith et al. 2010) benefits to individuals living in groups. However, hunting success does not increase at the same rate as group size increases (Schmidt and Mech 1997), and for gray wolves in the same population as this study, elk hunting success rates do not increase beyond packs sizes of approximately four wolves (MacNulty et al. 2012). Average pack size in the Northern Range is 9.9 (Smith et al. 2011); therefore, there must be some other driver influencing pack sizes to be larger than the size that maximizes hunting efficiency.

Competition with kleptoparasites is another possible explanation for sociality as smaller (African lions Caraco and Wolf 1975, Cooper 1991; gray wolves Vucetich 2004, Kaczensky 2005) and intermediate-sized groups (gray wolves Wilmers et al. 2003) lose more biomass to scavengers. Although Yellowstone wolves certainly lose carcass biomass to scavengers, they have usually finished their initial feeding before intensely interacting with some scavengers such as coyotes (Merkle et al. 2009) and bears (Gunther and Smith 2004). In general, Yellowstone wolves pay little attention to smaller

scavengers such as ravens (*Corvus corax*) and magpies (*Pica hudsonia*). Foraging efficiency may also be tied to territorial defense, especially in areas with low prey densities or high wolf densities as pack territories are more likely to overlap and packs have a higher chance of encountering a neighboring pack at a carcass. Kauffman et al. (2007) found the average catchability of prey (a measure of wolf territory quality) decreased during the initial ten years after wolf reintroduction due to the increase in number of packs and their selection of habitat to minimize conflict with other packs.

Packs normally consist of at least two unrelated adults and their offspring from several years (Mech 1970). This high level of relatedness within the group, and the assistance of nonbreeders in raising young, has prompted many to suggest kin-selection as a possible explanation for sociality (Schoener 1971; Rodman 1981; Hayes 2000; Schmidt and Mech 1997). Stahler et al. (2013) found that the number of pups born to a single female reached a maximum when adult pack size was eight, and the pack effect was the second-most-important factor to female reproductive success, after individual female weight. Although eight is very close to the average Northern Range pack size of 9.9, each year there are several large packs of 15 to 20 or more individuals (Yellowstone Wolf Project, unpublished data).

Packs larger than eight individuals may not produce as many pups, but they may be better at protecting them from harm as pup survival increases throughout all pack-size ranges (Stahler et al. 2013). Pusey and Packer (1994) found that female lions benefit from living in groups because they cooperatively defend their young against infanticide. Assumed to be a rare occurrence in wolf populations, infanticide does occur (Latham and Boutin 2011; Yellowstone Wolf Project, unpublished data). It may be difficult to

distinguish pup defense from resource (e.g., prey, territory) defense, as both are often responses to conspecific threats. Likely pup defense and resource defense are intertwined, with success in one leading to, or being a significant factor in, success in the other. Our results show that larger pack size is a key factor in a successful aggressive inter-pack interaction, likely for both possible drivers of territoriality.

Residency status. –Residency did not seem to have an effect on success during interactions, contrary to studies on other species by Davies (1978), Krebs (1982), Marden and Waage (1990), Alcock (2001), and Johnsson and Forser (2002). Studies showing that territory residents nearly always win contests against intruders have been challenged recently (Hyman 2004; Kemp and Wiklund 2004) suggesting residency for some species may not be as important as previously thought. The insignificance of residency status in our study may be due to the relatively small size of the study area, which included the territories of three to seven packs resulting in high wolf density, abundant prey, and territory overlap (Smith et al. 2011). Further, a vacancy from the loss of a breeder in one pack was usually filled by an individual from a nearby pack (von Holdt et al. 2008; D. R. Stahler personal comm.), suggesting that familiarity with a large portion of the study area was high for most packs. Thus an advantage due to landscape familiarity likely does not exist for this population. Conceivably areas with low wolf density and little overlap among territories (e.g., the Interior of YNP, Alaska, or the High Arctic) would see residents more likely to win interactions, taking advantage of their knowledge of the interaction's location.

Group composition. – I hypothesized that packs with more individuals in certain demographic categories would have an advantage over their opponents and be more likely to win an interaction. Of the demographic groups included in model selection—relative number of adult males, adult females, yearlings, prime-aged adults, old adults, grays, and breeders, the two remaining in the best reduced model were relative number of old adults and adult males.

Our results demonstrated that winning packs have more old pack members than their opponents. Having old pack members may be related to the tenures of wolf packs. Packs with the oldest tenures were those most likely to include one or both of the breeding pair, and sometimes more, in the “old adult” category. Such packs possess a great deal of collective experience and although not extensively studied in wildlife, extended human tenures increases trust in the leaders of basketball teams and has proven to help teams win more games (Dirks 2000). Age often has an effect on an individual’s willingness to participate in aggressive interactions (free-ranging dogs Pal et al. 1998; song sparrows [*Melospiza melodia*] Hyman et al. 2004; Japanese macaques Majolo et al. 2005; domestic dogs Cafazzo et al. 2010). While most studies examined ages in two classes—juvenile and adult, I used continuous ages—ranging from 0.15 to 10.55 years—and could therefore classify individuals into more detailed categories (i.e. pups, yearlings, prime-aged, and old-aged). MacNulty et al. (2009b), using continuous ages, found that age has a significant effect on individual hunting ability for this population of wolves, with hunting success starting to decrease at approximately 4 years of age. It is unknown if the same decrease is seen in individual fighting ability but because packs with older wolves are more likely to succeed during an inter-pack interaction, there may be a more-

complex relationship between age and fighting ability than age and hunting ability. That is, while territorial defense may motivate all pack members to fight, mate defense may stimulate the older (and likely the breeders) of a pack to fight beyond the age when they are at their prime physical abilities resulting in a later peak than hunting or no peak at all. Investigation into this topic in the future would greatly enhance the understanding of the motivations of aggression and their relationships to senescence.

Research on senescence, or aging, of many species (humans [*Homo sapiens*] Tanaka and Seals 2008; horses [*Equus ferus caballus*] Mota et al. 2005; domestic dogs Taubert et al. 2007; gray wolves, MacNulty et al. 2009b) suggests that animals suffer physical effects due to aging, making them more vulnerable to mortality. I predicted that packs with more prime-aged adults would be more likely to win, because prime-aged adults are at their physical peak, as demonstrated in hunting efficiency (MacNulty et al. 2009b). This variable was not included in the best model, possibly because the relationship between age and territorial behavior is more complex than that to hunting behavior.

Males are the more-aggressive sex in several species (e.g., humans Muller and Wrangham 2009; olive baboons MacCormick et al. 2012), except in some matrilineal, social species such as spotted hyenas (Boydston et al. 2001). Consequently, if pack sizes are equal, the pack with more-aggressive individuals—in this case, adult males—is more likely to win.

Wolves are sexually dimorphic with males larger and weighing more than females (Mech 1970; 2006; Butler et al. 2006; MacNulty et al. 2009a). This may have been an adaptation in response to competition among males for mating opportunities or to

aggressive group-territorial defense as our study shows packs with higher number of adult males were more likely to be successful. Stahler (2011) demonstrated that reproductive success was higher for females that lived in packs with more males and attributed this result to benefits associated with male effectiveness in hunting, offspring protection, and territorial contests. Our results showing male wolves are advantageous during aggressive interactions provides quantitative support to this conclusion.

I predicted that packs with more breeders would be more likely to win as breeders should be motivated by territory and mate defense, giving them extra incentive to fight or escalate during an interaction. Because relative number of breeders was not included in the best reduced model, it is possible breeders do not increase their aggression level simply because they are breeders, or that perhaps the division in the types of breeders in a pack (i.e. those who breed within the pack—whose mates are also pack members—and those who breed outside the pack) changes their behavior in opposing ways. This difference will be important to recognize in future studies on numerical assessments of pack breeders and their effects on wolf-pack ecology and social behavior.

Conclusions. –Our study shows larger packs have a strong advantage during inter-pack aggressive interactions. Further, packs with more old individuals and more adult males have higher odds of defeating their opponents. Although many recent studies have focused on numerical assessment among social mammals, I demonstrate that group size alone is not the only important factor in intergroup aggressive interactions. In wolves, it appears that group composition, specifically the presence of certain individuals (older adults and adult males) can influence a group's odds of winning an interaction just as

much, if not more, than group size alone. These results highlight the dynamic effect of group composition on the outcome of interactions by demonstrating that the quality of group members can have important influences on resource protection and, therefore, on many aspects of wolf ecology and life history. This information is of particular importance to those concerned with wildlife management as my results indicate the loss of a valuable individual can have serious impacts on the overall fitness and competitiveness of the group. It is possible these changes can result in group or population instability, affecting all aspects of wolf pack life history.

Consistent with results from many studies on social mammals, I demonstrate that larger relative group size is still an important factor in successful intergroup aggressive interactions. The evolution of sociality among carnivores has many possible, likely interacting, explanations, but the importance of relative group size in successful territorial defense strongly suggests group-living may have evolved and may be maintained in response to large groups' superior abilities to protect themselves and their resources.

Table 1-1. Social species which exhibit territorial behavior in the form of intergroup aggression.

Species	Scent-mark	References
African lion (<i>Panthera leo</i>)	Y	Schaller 1972; Packer 1986; Heinsohn and Packer 1995; Heinsohn et al. 1996; Heinsohn 1997; Mosser and Packer 2009
Gray wolf (<i>Canis lupus</i>)	Y	Mech 1970; Mech 1973; Peters and Mech 1975
Ethiopian wolves (<i>Canis simensis</i>)	Y	Sillero-Zubiri and MacDonald 1998
Coyote (<i>Canis latrans</i>)	Y	Camenzind 1978; Barrette and Messier 1980; Bowen 1982; Bekoff and Wells 1986; Allen et al. 1999; Gese 2001
African Wild Dogs (<i>Lycaon pictus</i>)	Y	Creel and Creel 1995
Free-ranging dog (<i>Canis familiaris</i>)	Y	Pal et al. 1998; Cafazzo et al. 2010; Bonanni et al. 2010; Bonanni et al. 2011
Brown hyena (<i>Hyaena brunnei</i>)	Y	Owens and Owens 1979; Mills 1990
Spotted hyena (<i>Crocuta crocuta</i>)	Y	Kruuk 1972; Mills 1990; Henschel and Skinner 1991; Boydston et al. 2001
Banded mongoose (<i>Mungos mungo</i>)	Y	Rood 1983; Cant 2002; Furrer et al. 2011
Dwarf mongoose (<i>Helogale parvula</i>)	Y	Rood 1983; Rasa 1989
Meerkat (<i>Suricata suricatta</i>)	Y	Doolan and MacDonald 1996
Common marmoset (<i>Callithrix jacchus</i>)	Y	Lazaro-Perea 2001
Black and white colobus monkey (<i>Colobus guereza</i>)	N	Fashing 2001; Sicotte and MacIntosh 2004; Harris 2010
Chimpanzee (<i>Pan troglodytes</i>)	N	Watts and Mitani 2001; Wilson et al. 2001; Wilson et al. 2002; Wrangham 2006; Mitani et al. 2010; Wilson et al. 2012

Table 1-2. Pearson's correlation coefficient (r) between covariates. The dark shaded cells indicate $r > 0.7$ or < -0.7 and has strong correlation; the lighter shaded cells indicate $r < 0.7$ and > 0.4 or > -0.7 and < -0.4 and has a moderate correlation. Unshaded cells have low or no correlation ($r < 0.4$ and > -0.4). Covariates with strong correlation to RPS were not included in model building in order to avoid biased coefficients.

Pearson's correlation coefficient (r) between covariates													
	RPS	males	females	pups	yearlings	prime-aged	old	gray	black	adult males	adult females	resident	breeders
RPS	1.000												
males	0.724	1.000											
females	0.851	0.417	1.000										
pups	0.875	0.577	0.776	1.000									
yearlings	0.549	0.506	0.435	0.199	1.000								
prime-age adults	0.535	0.456	0.445	0.387	0.067	1.000							
old adults	0.231	0.124	0.311	0.145	0.107	-0.192	1.000						
grays	0.621	0.624	0.304	0.511	0.388	0.406	-0.008	1.000					
blacks	0.835	0.498	0.878	0.761	0.431	0.405	0.306	0.100	1.000				
adult males	0.420	0.739	0.098	0.166	0.519	0.460	-0.046	0.492	0.210	1.000			
adult females	0.679	0.326	0.817	0.413	0.604	0.388	0.402	0.258	0.689	0.084	1.000		
residents	0.022	-0.029	0.112	-0.022	0.056	-0.044	0.271	-0.096	0.112	-0.088	0.206	1.000	
breeders	0.573	0.422	0.604	0.441	0.206	0.505	0.405	0.251	0.559	0.247	0.593	0.103	1.000
nonbreeders	0.947	0.696	0.811	0.869	0.579	0.452	0.121	0.620	0.780	0.413	0.611	0.026	0.355

Table 1-3. Models of the relative influence of age categories (without RPS [Model A] and with RPS [Model B]) and sex of adults (without [Model C] and with RPS included [Model D]) on winning an interaction (not including variables with high correlation to RPS).

Model	Variable	Coefficient	SE	Z	P>z	95% Confidence Interval	
Model A: Age categories without RPS	yearlings	0.714	0.196	3.64	0.000	0.330	1.098
	prime-age adults	0.773	0.215	3.60	0.000	0.352	1.194
	old adults	1.380	0.416	3.32	0.001	0.564	2.196
	constant	0.268	0.434	0.62	0.538	-5.840	1.120
Model B: Age categories with RPS	RPS	0.947	0.304	3.11	0.002	0.351	1.543
	yearlings	0.609	0.316	1.93	0.054	-0.016	1.228
	prime-age adults	0.204	0.278	0.74	0.462	-0.340	0.749
	old adults	1.333	0.641	2.08	0.038	0.076	2.589
Model C: Sex of adults without RPS	constant	0.423	0.741	0.57	0.568	-1.029	1.876
	adult males	0.812	0.200	4.06	0.000	0.420	1.204
	adult females	0.920	0.207	4.46	0.000	0.516	1.325
	constant	0.282	0.402	0.70	0.482	-0.505	1.069
Model D: Sex of adults with RPS	RPS	0.735	0.233	3.15	0.002	0.277	1.192
	adult males	0.687	0.278	2.47	0.014	0.142	1.232
	adult females	0.413	0.259	1.59	0.111	-0.095	0.921
	constant	0.244	0.630	0.39	0.699	-0.990	1.478

Table 1-4. Variables measured during aggressive interaction data collection.

Variable	Included in saturated model	Description
RPS	Y	numerical (range -22 to 16)
residents	Y	coded (A=residents, B=intruders, C=in territory overlap)
males	N*	numerical (range -7 to 8)
females	N*	numerical (range -14 to 11)
pups	N*	numerical (range -19 to 10)
yearlings	Y	numerical (range -6 to 9)
prime	Y	numerical (range -6 to 6)
old	Y	numerical (range -3 to 4)
grays	Y	numerical (range -10 to 11)
blacks	N*	numerical (range -14 to 14)
adult males	Y	numerical (range -6 to 7)
adult females	Y	numerical (range -7 to 10)
breeders	Y	numerical (range -6 to 6)
nonbreeders	N*	numerical (range -20 to 14)

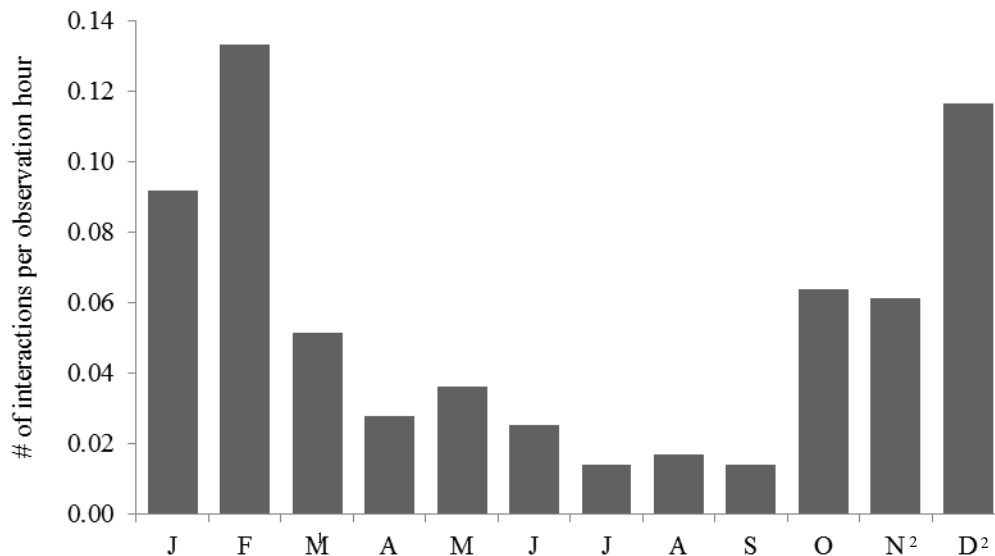
The variables include relative pack size (RPS), residency status (residents), and relative number of males, females, pups, yearlings, prime-aged adults, old adults, grays, blacks, adult males, adult females, breeders, and nonbreeders.

*Not included in saturated model because variable was highly correlated to RPS ($r > 0.7$).

Table 1-5. Best-fit model from backward stepwise selection of saturated model using logistic regression analysis of select variables and successful interaction outcome (WIN).

Model results from the best model according to backward stepwise selection							
Variable	Odds Ratio	Coefficient	SE	Z	P>z	95% Confidence Interval	
RPS	2.425	0.886	0.255	3.47	0.001	0.385	1.386
relative old adults	2.505	0.918	0.468	1.96	0.050	0.002	1.835
relative adult males	1.651	0.501	0.235	2.14	0.033	0.041	0.961
constant	1.150	0.139	0.648	0.22	0.830	-1.131	1.410

Figure 1-1. Number of aggressive interactions per observation hour by month for all years combined (1995-2010).



¹March number of interactions was adjusted (divided by 2.0) because of increased observer effort—twice as many observation hours ($n = 720$) compared to average observation hours per month ($n = 360$).

²November and December number of interactions was adjusted (divided by 1.5) because twice as many observation hours for 15 out of the 30 days of the two months ($n = 540$).

Figure 1-2. Relative pack size and outcome (win or lose) of pack-pack interactions (n=121).

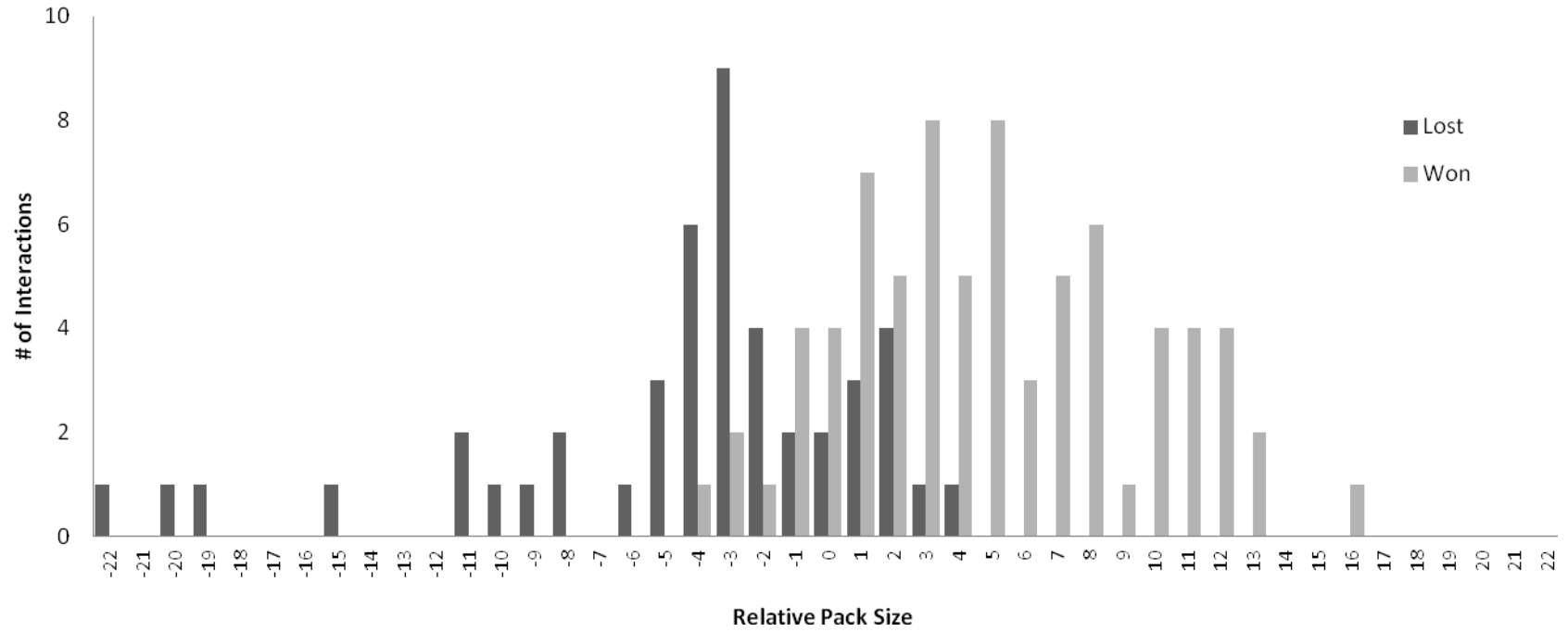


Figure 1-3. Number of fatal interactions and relative size of packs experiencing an intraspecific mortality (n=43, 1995-2010). Pack sizes are estimates of total pack size based on consistent observations before and after the date of the mortality. Most often a wolf-killed wolf was found based on its mortality signal. Then I inferred the identity of the attacking pack based on its known location relative to the dead wolf.

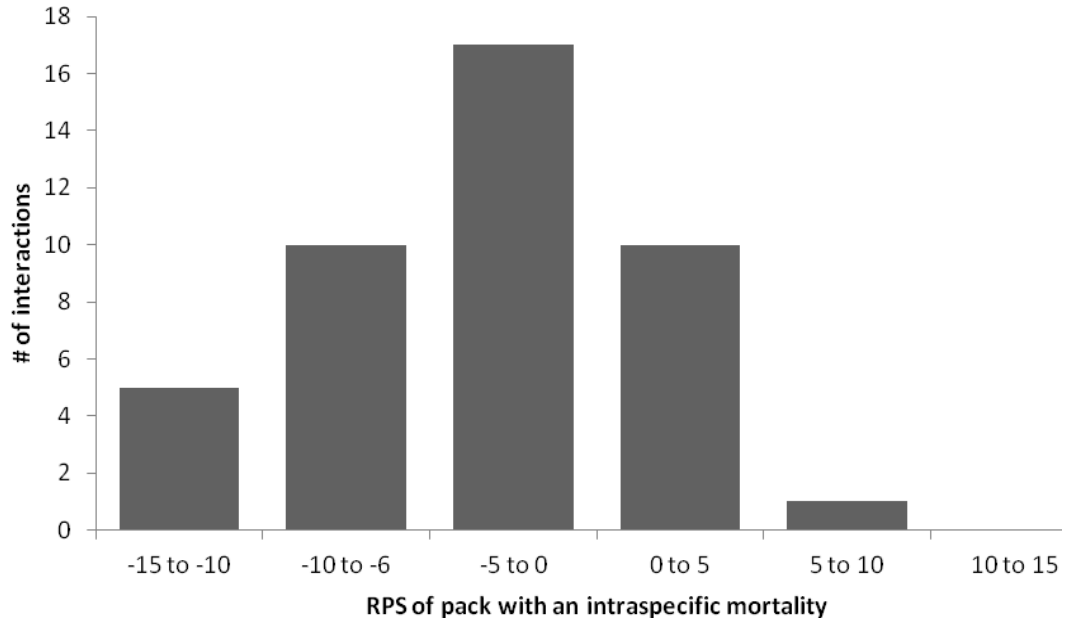
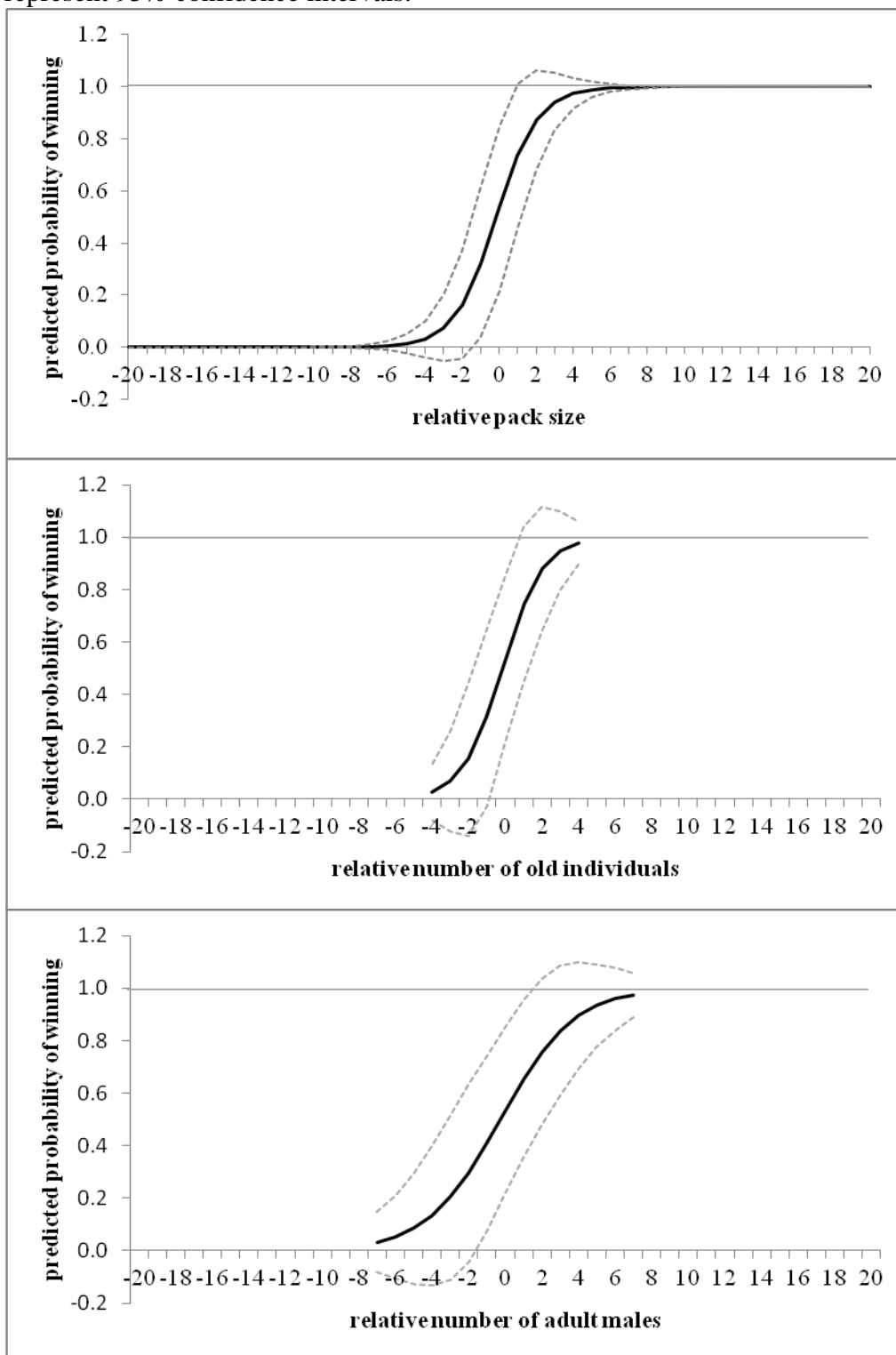


Figure 1-4. Predicted values of the probability of a pack winning and one of the three terms from the best fit model—holding the other two terms fixed. Gray, dashed lines represent 95% confidence intervals.



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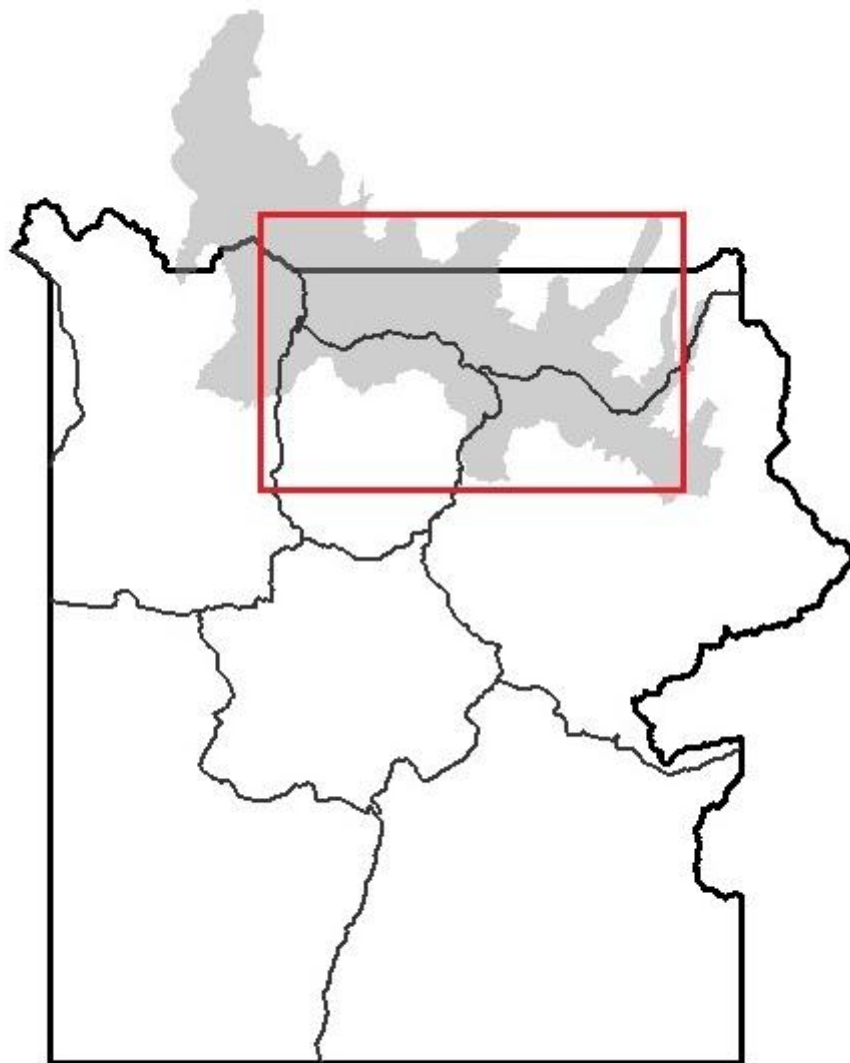
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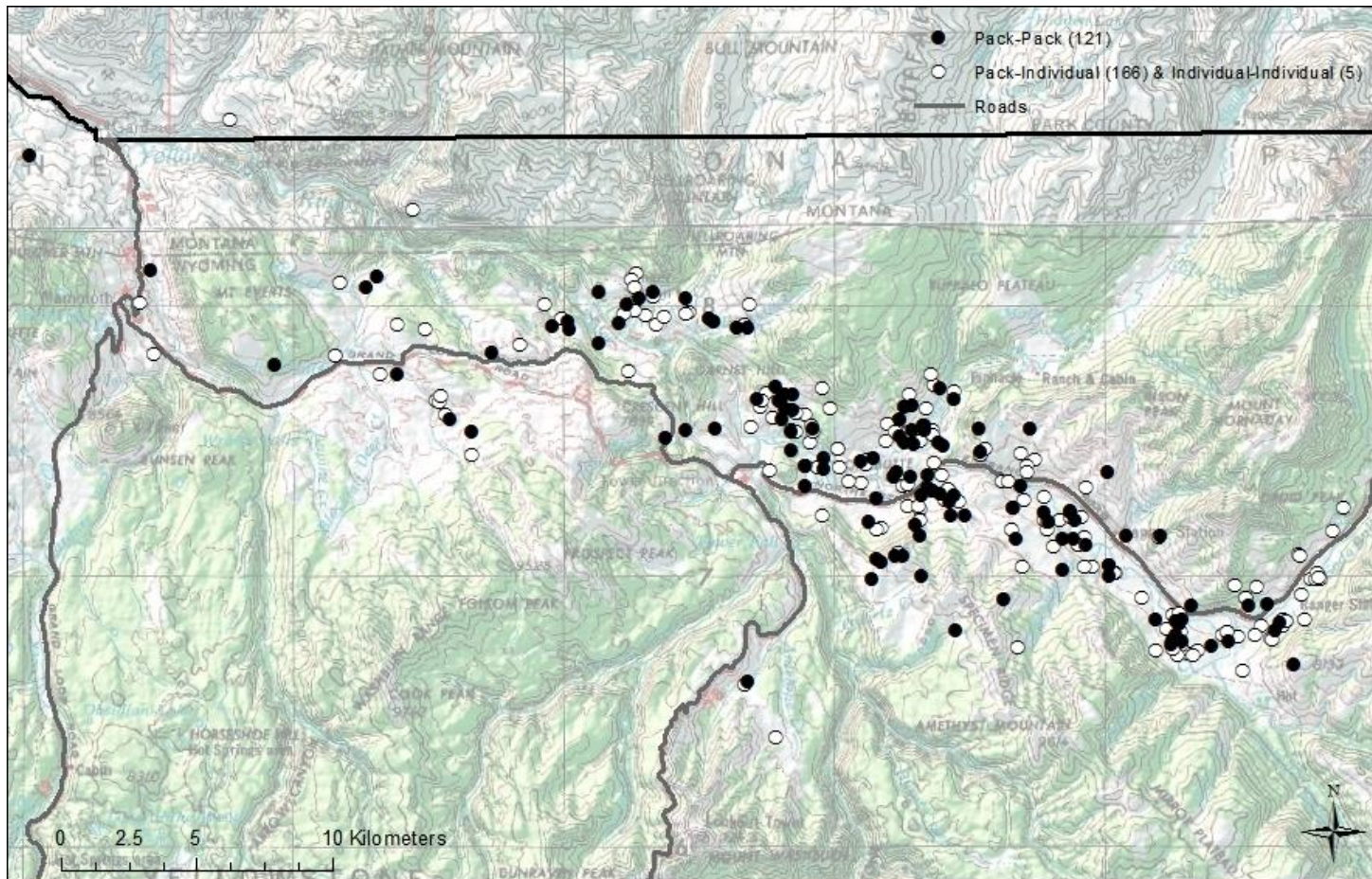
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APPENDICES

Appendix A. Boundary of Yellowstone National Park, Wyoming, with the Northern Range (shaded) and study area (boxed).

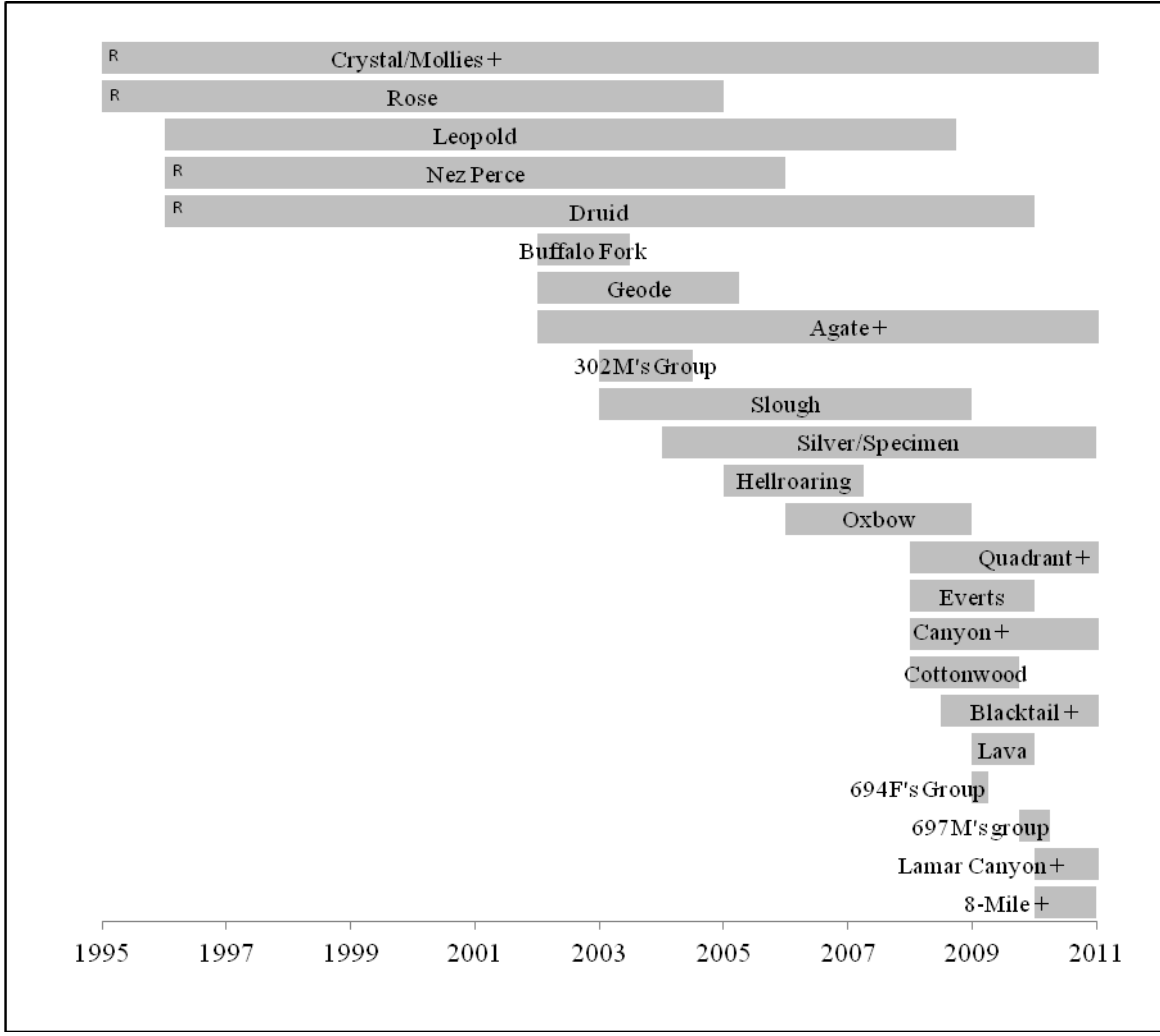


Appendix B. Map of the study area with pack-pack interactions (black) and pack-individual interactions (white)¹.



¹ Note that the locations of these interactions are biased as most observations were made from areas close to the road.

Appendix C. Tenures of pack with at least one observed inter-pack aggressive interaction during the study, biological years 1995 through 2010.



^R Pack released as part of reintroduction effort. All other packs formed naturally.
⁺ Pack still in existence at the end of the study (1 April 2011).

Appendix D. Pack compositions at beginning of the biological year (15 April).

biological yr	pack name	interactions	won	lost	pack size	males	females	yearlings	prime-age adults	old adults	breeders	nonbreeders
1995	Crystal	1	0	1	6	5	1	2	3	1	0	6
1995	Rose	1	1	0	3	1	2	1	2	0	2	1
1996	Druid	2	0	2	5	1	4	3	0	2	0	5
1996	Rose	2	2	0	9	4	5	7	1	1	3	6
1999	Rose	2	1	1	17	8	7	8	7	2	3	14
1999	Druid	3	1	2	7	2	5	1	6	0	2	5
1999	Crystal	1	1	0	15	7	4	8	6	1	2	13
1999	Leopold	1	1	0	9	5	4	4	5	0	2	7
2000	Rose	3	0	3	10	5	5	2	7	1	3	7
2000	Druid	4	4	0	8	3	5	2	6	0	3	5
2000	Tower	1	0	1	3	2	1	0	3	0	3	0
2001	Druid	8	8	0	23	8	15	20	4	2	4	22
2001	Nez Perce	3	0	3	11	8	3	7	10	0	2	17
2001	Agate	2	0	2	4	2	2	1	2	0	3	1
2001	Geode	1	0	1	6	2	4	3	3	0	2	4
2001	Buffalo Fork	1	0	1	3	1	1	0	3	0	2	0
2002	251F Group	2	1	1	2	1	1	0	2	1	2	0
2002	302M Group	1	0	1	2	1	1	0	2	0	2	0
2002	Agate	1	0	1	6	2	4	1	5	0	4	2
2002	Buffalo Fork	1	1	0	3	1	1	0	3	0	2	0
2002	Druid	12	11	1	15	7	6	7	5	2	4	11
2002	Geode	3	3	0	6	2	4	0	6	0	2	4
2002	New Group	8	3	5	4	2	2	1	3	0	4	0
2002	Mollie's	3	1	2	10	8	2	6	4	0	2	8
2002	Slough	9	1	8	5	3	2	0	5	0	5	0
2003	255F' Group	2	0	2	2	1	1	0	2	0	2	0
2003	302M Group	1	0	1	3	1	2	0	3	0	2	1
2003	Agate	5	1	4	7	2	4	3	2	2	3	4
2003	Druid	12	9	3	9	3	6	2	5	2	5	4
2003	Geode	1	1	0	8	5	3	2	5	1	3	5

Table of pack compositions (continued)

biological yr	pack name	interactions	won	lost	pack size	males	females	yearlings	prime-age adults	old adults	breeders	nonbreeders
2003	New Group	2	0	2	4	2	2	1	3	0	4	0
2003	Slough	5	2	3	5	3	2	0	5	0	3	2
2003	Specimen Rg	1	1	0	3	2	1	0	3	0	2	1
2004	Agate	2	0	2	7	4	3	4	2	1	2	5
2004	Druid	10	9	1	14	9	5	9	4	1	3	11
2004	Geode	5	1	4	6	2	4	1	4	1	3	3
2004	Leopold	5	3	2	17	7	6	6	7	0	3	11
2004	Mollie's	1	0	1	7	6	1	2	4	1	2	5
2004	Slough	7	4	3	12	6	4	4	8	0	4	8
2004	Specimen Rg	1	0	1	3	2	1	0	2	1	2	1
2005	Agate	1	0	1	7	4	3	2	4	1	2	5
2005	Hellroaring	2	1	1	6	5	1	0	6	0	0	6
2005	Leopold	4	4	0	25	3	7	3	7	0	3	7
2005	Oxbow	2	0	2	4	1	3	2	1	1	4	0
2005	Slough	2	2	0	15	7	8	6	8	0	8	7
2006	Agate	4	4	0	7	3	4	2	4	1	2	5
2006	Druid	2	2	0	4	2	2	0	3	1	4	0
2006	Hellroaring	2	0	2	6	6	0	0	6	0	1	2
2006	Leopold	1	1	0	7	2	5	3	2	2	2	5
2006	Mollie's	1	0	1	7	6	1	0	6	1	4	3
2006	Oxbow	1	0	1	4	1	3	0	3	1	4	0
2006	Slough	3	0	3	12	4	8	3	7	2	6	6
2007	Agate	4	4	0	12	5	7	6	4	2	3	9
2007	Cottonwood	3	0	3	2	1	1	0	1	1	2	0
2007	Druid	3	3	0	11	4	7	8	2	1	2	9
2007	Hayden	1	1	0	4	1	3	1	1	2	3	1
2007	Leopold	2	0	2	15	1	7	3	3	2	2	6
2007	Oxbow	2	1	1	11	3	4	8	3	0	2	9
2007	Silver	2	0	2	3	1	2	0	2	1	2	1
2007	Slough	6	4	2	9	2	7	0	9	0	6	3

Table of pack compositions (continued)

biological yr	pack name	interactions	won	lost	pack size	males	females	yearlings	prime-age adults	old adults	breeders	nonbreeders
2008	Agate	2	1	1	14	4	10	8	5	1	2	11
2008	Blacktail	1	0	1	10	6	4	7	2	1	6	4
2008	Cottonwood	1	0	1	2	1	1	0	1	1	2	0
2008	Druid	4	4	0	16	7	9	7	7	2	8	7
2008	Oxbow	1	0	1	6	3	3	8	7	0	2	13
2008	Slough	4	2	2	15	3	12	9	6	0	5	10
2009	694F Group	1	0	1	3	1	2	1	2	0	3	0
2009	697M Group	2	1	1	3	2	1	0	3	0	3	0
2009	Agate	4	1	3	4	2	2	0	4	1	3	2
2009	Blacktail	1	1	0	6	4	2	0	5	1	4	2
2009	Cottonwood	1	1	0	5	3	2	0	4	1	2	3
2009	Druid	6	4	2	14	4	10	5	8	1	3	11
2009	Everts	1	1	0	6	2	4	3	2	1	2	4
2009	Lamar	1	0	1	3	2	1	2	1	0	2	1
2009	Lava	3	0	3	3	1	2	0	2	1	3	0
2009	Mollies	1	1	0	14	5	6	3	10	1	2	12
2009	Silver	1	1	0	3	1	2	1	0	2	2	0
2010	8-Mile	1	1	0	6	3	3	4	2	0	2	4
2010	Agate	1	1	0	4	2	2	0	2	2	3	0
2010	Blacktail	2	2	0	10	4	6	4	6	0	6	4
2010	Canyon	1	0	1	3	2	1	0	3	0	3	0
2010	Quadrant	1	0	1	7	2	5	3	2	2	3	0