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Canis Lupus (Gray Wolf) Pup Survival in Yellowstone National Park

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ABSTRACT The aim of this study was to describe gray wolf (*Canis lupus*) pup survival rates throughout the summer months in Yellowstone National Park. Understanding pup survival has implications for trends in pack and population age structure, cooperative breeding ecology and other breeding tendencies, social hierarchies, and population fitness, among other elements of species-specific population ecology. A general understanding of trends in pup survival is also relevant to state and federal land that allow gray wolf harvest. Understanding such trends and survival ecology gives managers and biologists the opportunity to evaluate gray wolf populations at a more comprehensive level and implement more effective management decisions. This study analyzed how pup survival rates vary temporally and spatially throughout Yellowstone's Northern Range and some interior locations. Data was quantified using field notes from Yellowstone Wolf Project staff, focusing on the months May through September, and years 2009 and 2010. The data was originally collected and recorded from direct observation of wolves by Wolf Project staff and other diligent citizen scientists. Using this data, I quantified number of observed breeding wolf packs, and pup high counts and survival rates specific to each pack. This report includes spatial information specific to Yellowstone regarding temporal trends in pup survival in the form of visual maps. My analyses found that high counts by pack did differ

throughout the observational period in both years, survival rates in 2009 varied by pack and did not vary in 2010, though survival rates between packs were not statistically significant.

KEY WORDS *Canis lupus*, gray wolf, pup, survival, Yellowstone National Park.

INTRODUCTION

After gray wolves (*Canis lupus*) were eradicated from Yellowstone National Park in the mid-1930s, discussion began 40 years later (1972) to re-establish a wolf population in Yellowstone (Phillips and Smith 1997). By 1994, an interagency Environmental Impact Statement was completed, initiating the wolf reintroduction process (Phillips and Smith 1997). To meet the program criteria, biologists determined that, as a direct result of the reintroduction, a minimum of 10 packs must produce pups for 3 successive years (Phillips and Smith 1997:5-6), indicating that recruitment (and, in turn, pup survival) was critical to population establishment from both a legal and biological standpoint.

In 1995 and 1996, 31 wolves were successfully relocated from Canada to Yellowstone (Phillips and Smith 1997:9). Within the first 2 years following reintroduction, 23 wolf pups were born (amongst 8 packs), 5 of which died (Phillips and Smith 1997:9), producing a pup survival rate of approximately 78 percent, which is slightly higher than the overall survival rate in the 24 years since reintroduction (Figure 1, R. McIntyre, personal communication, M. Metz personal communication). From early on in the project, pup survival was designated as a critical focus (Phillips and Smith 1997:8). Since reintroduction, biologists and field technicians have diligently recorded data and field notes regarding pup counts, pack affiliation, adult presence, and coat coloration.

Pup Data

Most existing pup datasets, however, are minimal and lack detail. The lack of thorough datasets are, in part, due to limitations in pup detection. A 2013 study completed by Stahler et al. considered characteristics of pup survival, though the study did not account for variation based on detection probability. Thus, a comprehensive and detailed approach is essential to understanding intricacies of pup survival and fatalities, while considering detection deficits. At easily accessible den sites, pup observations occur almost daily, and this observation data is used to produce a relatively thorough encounter history. Past and current data has primarily produced monthly pup survival rates (Figure 1, M. Metz personal communication); in order to expand on this data, this study included more observation information, including adult and pup demographic data present at the site, location, observer, individual collared wolf identification, and other circumstantial, qualitative comments.

Effects of Social Dynamics and Pup Ecology

Wolves are highly social animals and rely heavily on social structure and caregiving amongst pack members to sustain individual health and pack recruitment (Ausband et al. 2017, Yellowstone National Park 2018*a*:216). Generally, each pack includes a dominant alpha male and female with several subordinate members (Yellowstone National Park 2018*a*:216). Wolves employ a cooperative breeding strategy, meaning that some subordinate members, or 'helpers,' are responsible for providing the mother wolf and pups with food while they are confined to the den in the pups' first days of life (Ausband et al. 2017). As pups retreat from the den, helpers may be responsible for continuing to provide food in the form of regurgitations. The presence and behavior of helpers may contribute to adult or pup survival or otherwise wellbeing (Ausband et al. 2017).

Effects of Disease

Disease has been known to have significant implications for survival of both adults and pups in Yellowstone. Canine distemper, infectious canine hepatitis, canine parvovirus, Sarcoptic mange, and bordetella have been historically present in Yellowstone's wolf populations, with known distemper outbreaks occurring in 2005, 2008, and 2009 (Yellowstone National Park 2018*a*:217). The 2005 outbreak decimated pup counts, killing two-thirds of all pups born that year (Yellowstone National Park 2018*a*:217). Mange was also widely prevalent in 2009 (Yellowstone National Park 2018*a*:217), thus, it is not unlikely that the 2009 mange or distemper outbreaks contributed to pup mortality in 2009.

Effects of Prey Availability

In Yellowstone, wolves mainly prey on elk, though deer, pronghorn, and bison also make up a slight portion of their diet (Smith et al. 2010:12, Yellowstone National Park 2018*a*:216). Wolves mostly target young and weak elk as prey, though in 2009, it was thought that a decrease of individual weak elk affected total volume of food consumption, which caused one adult wolf to die from malnutrition, an otherwise unlikely event in the park (Smith et al. 2010:2). However, it was found that total biomass consumed had not significantly fluctuated from previous years, though kill rates had, in fact, decreased (Smith et al. 2010:12). In the 2008 to 2009 winter season, the Northern Yellowstone Cooperative Wildlife Working Group estimated that approximately 7100 elk occupied the northern range, and from 2009 to 2010, the population dropped to approximately 6000 individuals (Yellowstone National Park 2018*b*). It is thought that prey availability has a significant impact on wolf survival, which may have direct or indirect implications for pup care and survival (via changes in frequency of regurgitations, for example).

RESEARCH QUESTIONS

Question 1: Pup Dynamics Across Time and Space

This study analyzed 2 major questions. First, I wanted to understand how pup dynamics change across both spatial and temporal scales, and further, how basic pack demographic elements may impact these dynamics. To examine this, I was interested in understanding how pup high counts (maximum number of pups observed over a specified time period) and pup survival varied between years and varied with pack affiliation. I predicted that both pup high count and survival would vary between packs.

Question 2: Detection Probability

Due to the heavy reliance on physical observation of pups in Yellowstone, I wanted to understand whether ground detection probability intersects our ability to both observe pups in the field and analyze population metrics (i.e. calculating apparent survival rate[1]). Further, I wanted to analyze how pup high counts change throughout the season. I predicted that as the season progressed and pups grew to become more independent, high counts would slowly increase throughout the first few months, before apparent decreases in survival became noticeable (indicated by a drop in pup high count). I expected that individual pups would become intermittently more visible throughout the first month to two months of life, possibly due to differences in growth, ability, and willingness to depart from caregivers, resulting in incomplete pup counts (due to lack of visibility). Then, I expected that as all pups progressed out of the complete dependence stage, all of the pups would become visible, and more complete and accurate high counts would result. Finally, I expected that subsequent decreases in high counts

[1] Used to represent a survival rate calculated based on a partial time segment of the designated age class (rather than calculating survival based on the entire length of the designated age class) and signifying an inherent slight ambiguity.

could likely be attributed to decreases in apparent survival, since the apparent high count had already been reached.

STUDY AREA

Reintroduction and Recovery Era

In 1971, Yellowstone National Park officials, amongst other attending agencies, held the first formal meeting to discuss the reintroduction of wolf populations in the park, following recent wolf activity in the Greater Yellowstone Area (Bangs and Fritts 1996). During this non-wolf era, Yellowstone's immense elk population was causing ecological deficits, including significant impacts to soil, plants, and other wildlife (Ripple and Beschta 2012). This meeting incited local field work aimed at determining whether wolves still existed within park boundaries (i.e. from immigration into the park), though the findings returned negative (Bangs and Fritts 1996). Following this determination, a formal recovery plan was instated to stimulate plans for wolf restoration and recovery (Bangs and Fritts 1996).

In 1994, the National Park Service (NPS) released the final copy of the reintroduction Environmental Impact Statement, classifying the Yellowstone wolf population as a nonessential experimental population (Bangs and Fritts 1996). Following the March 1995 release, 2 of 3 packs produced pups, and in April of 1996, 4 total packs produced pups (Phillips and Smith 1997:16-17). As individual packs expanded, failed, shifted ranges, and so forth, packs began to occupy both Northern Range and interior locations. Some packs have predominantly existed throughout the Hayden Valley and Canyon Area, while others began to expand into Bechler, the area surrounding Yellowstone Lake, and Pelican Valley. Eventually, some pack territories straddled or moved entirely outside of park boundaries.

Study Years

In 2009, the total number of wolves in Yellowstone significantly decreased from the year prior, with a total of 96 wolves amongst 14 packs, 1 group, and 2 individual wolves not affiliated with a pack (Smith et al. 2010:*v*), according to the 2009 Wolf Project Report. Of the 96 wolves, 12 individuals (6 pairs) bred (Smith et al. 2010:*v*). Towards the end of the 2009 season, mange became significantly present in sections of the population, causing the dismount of the Druid Peak Pack (Smith et al. 2011:7). A total of 8 packs and groups lived in the Northern Range (682M Group, Agate, Blacktail, Cottonwood, Druid, Everts, Lava Creek, and Quadrant Mountain), 2 of which produced pups (Blacktail and Quadrant Mountain), and 8 packs lived in non-Northern Range interior locations (Bechler, Canyon, Cougar Creek, Gibbon Meadows, Grayling Creek, Mollie's and Yellowstone Delta), 4 of which produced pups (all but Bechler, Canyon, and Yellowstone Delta, Smith et al. 2010:1).

In 2010, the total number of Yellowstone wolves slightly increased from the year prior, though the total number of packs dropped (Smith et al. 2011:1). A total of 97 wolves comprised 11 packs with 6 remaining non-affiliated wolves (Smith et al. 2011:1). A total of 4 packs occupied the Northern Range (Agate, Blacktail, Lamar Canyon, and Quadrant Mountain), 3 of which produced pups (all but Quadrant Mountain) and 7 packs lived in interior locations (Bechler, Canyon, Cougar Creek, Grayling, Mary Mountain, Mollie's, and Yellowstone Delta), of which 5 produced pups (all but Cougar Creek and Grayling, Smith et al. 2011:3).

METHODS

Field Methods

In Yellowstone, wolf pups are not collared until at least 6 months of age[2], though pups may be collared during their first winter (B. Cassidy, University of Montana, thesis proposal). Prior to radio collaring, pup data is entirely reliant on aerial and ground observation[3], creating detection and observation intricacies, especially when newborn and young pups are incapable of moving far from the den or are based at remote den sites (B. Cassidy, University of Montana, thesis proposal). Data collection methods, however, have been relatively consistent since 1995 (B. Cassidy, University of Montana, thesis proposal), including field notes with thorough accounts of daily wolf observations.

Data quantification for this project relied solely on field notes from Wolf Project biologist and former National Park Service employee Rick McIntyre. McIntyre's daily field notes provided thorough accounts of each wolf observation in addition to reports from visitors and diligent citizen scientists, cordially referred to as 'wolf watchers.'

Data Quantification

Using McIntyre's field notes from 2009 and 2010, I quantified wolf pup observations from May 1 through September 30 to create a detailed encounter history of each observed pack. To qualify as an observation, 1 or more wolf pups needed to be observed. From there, each quantified observation included as much of the following data available in the notes: date and time, pup and adult count and coloration of each, pack or group affiliation, den/rendezvous site, observer, identification numbers of individual collared wolves present, and additional comments.

Statistical Methods

[2] Wolves are considered pups from 0 to 12 months of age.
[3] This study will only analyze ground observations.

High counts were calculated each week (for a total of 23 weeks) throughout the entirety of the summer season. Apparent survival rate by pack was calculated using the maximum pup high count at the beginning and end of the observation period. Observation period is used to designate the time period within the full summer season that the pack was actually observed. In order to account for potential deficits in detection probability, a 4 week buffer period was used to determine initial and final pup high counts. Within each buffer period, the highest count was selected. For nearly all packs, in both years, the initial high count was derived from the first 4 weeks of observation for that specific pack (beginning with the first week pups were observed, followed by the 3 weeks after the initial observation), and the final high count was derived from the last 4 weeks of observation for that pack (ending with the last week pups were observed, in addition to the 3 weeks prior to the final observation). For packs with 8 or less weeks between the initial and final observations, the length of the initial and final periods were calculated by dividing the total number of weeks in the observational period in half, and allocating the first half to the initial period and the final half to the final period. Finally, survival rate was calculated by dividing the final high count by the initial high count. Standard error was calculated using a count encompassing all of the specified pack observations. Variance in survival rates amongst packs and p-value was calculated using a single factor analysis of variance (ANOVA).

Mapping

QGIS software was used to create visual maps representing survival rate for each pack. Using published Wolf Project pack territory maps (Smith et al. 2010:*vi*, Smith et al. 2011:2), territory data was georeferenced with existing geographic data (Wyoming State Geological Survey) to develop shapefiles indicating territory boundaries. Using territory polygons to distinguish between packs, graduated color symbology was applied to individual packs to represent apparent pack survival.

RESULTS

2009 Results

In 2009, an initial high count of 21 pups in 5 packs were observed by ground observation in the months of May through September. Of those 21, there were initially 6 pups in the Blacktail Pack (Figure 2), 1 pup in the Canyon Pack (Figure 3), 4 pups in the Cottonwood Pack (Figure 4), 7 pups in the Druid Pack (Figure 5), and 3 pups in the Quadrant Pack (Figure 6). Both Canyon and Quadrant retained 100 percent apparent pup survival throughout the summer season (Figures 7 and 8). Canyon was observed from week 10 through the final week (Figure 3), and Quadrant was observed from week 12 through week 19 (Figure 6). Blacktail was observed from the week 8 through the final week (Figure 2), and lost 1 pup, concluding with an apparent pup survival rate of 83.3 percent (Figures 7 and 8). Cottonwood was observed from week 2 through week 21 (Figure 4), and lost 3 pups, concluding with an apparent pup survival rate of 25.0 percent (Figures 7 and 8). Druid was observed from week 8 through the final week (Figure 5), concluding with an apparent pup survival rate of 57.1 percent (Figures 7 and 8).

2010 Results

In 2010, an initial high count of 26 pups in 7 packs were observed by ground observation in the months of May through September. Of those 26, there were initially 5 pups in the Agate Pack (Figure 9), 6 pups in the Blacktail Pack (Figure 10), 3 pups in the Canyon Pack (Figure 11), 3 pups in the Cougar Creek II Pack, 4 pups in the Lamar Canyon Pack (Figure 12), 1 pup in the Mollie's Pack (Figure 13), and 4 pups in the Silver Pack (Figure 14). All packs retained 100 percent apparent survival throughout the summer season (Figures 15 and 16). Agate was observed from week 19, with 3 observed pups, through week 21, finishing with 5 total observed pups (Figure 9). Blacktail was observed from week 5, with 3 observed pups, through week 22, finishing with 6 observed pups (Figure 10). Canyon was observed from week 10 through the final week, with 3 pups observed consistently throughout the season (Figure 11). Cougar Creek II was observed once with 3 pups in week 18 and was not included in the survival analysis. Lamar Canyon was observed from week 3 through the final week, with 4 pups observed consistently throughout the season (Figure 12). Mollie's was observed twice in weeks 17 and 23 with 1 pup present each time (Figure 13). Silver was observed from week 8 through week 13, with 4 pups observed throughout the observation period (Figure 14).

2009 and 2010

The Blacktail and Canyon packs were the only packs observed in both seasons. While Canyon remained at 100 percent survival in both seasons ($\bar{x} = 1.00$; $\sigma^2 = 0$)[4], Blacktail showed an increase from 83.3 percent survival in 2009 to 100 percent survival in 2010 ($\bar{x} = 0.92$; $\sigma^2 = 0.01$). Survival rates between packs were not statistically significant (*p-value* = 0.09; $\alpha = 0.05$), and the survival null hypothesis could not be rejected.

DISCUSSION

Analyses

Results of the study indicate that while there is apparent variation amongst both high counts and survival rates, differences in survival rates between packs are insignificant. It is possible that increased observations and instituting mitigations for detection probability deficits

[4] $\bar{x}$ denotes sample mean; σ^2 denotes variance.

may alter the analysis outcomes. However, it is important to note that in 2010, high counts increased after the first (or first several) observation(s) in 2 out of 6 packs, indicating that detection probability (towards the beginning of the observation period/denning season) may play a role in both observing pups and analyzing survival metrics. In 2009, however, high counts did not increase during the initial observational period. It is possible, though, that fatalities occurred in or near the den that were not observed (via a decrease in high count) or discovered otherwise.

The cause of low pup survival rate in 2009 has historically been perceived as a mystery (B. Cassidy personal communication). In Metz's pup survival figure (Figure 1, M. Metz personal communication), 2009 is displayed as the fourth lowest pup survival year since reintroduction. Both disease and harvest were widely present throughout some wolf packs in the park. Many Druid adults and at least one pup fell victim to mange in the mid-summer months, and several Cottonwood adults were harvested in early to mid-September. It is possible that disease affected the health of both the adults and pups and inadvertently affected the care of the pups. It is also possible that the harvest of adults may have impacted care to pups.

Management Implications

Understanding differences (or similarities) in high counts and pup survival throughout Yellowstone has implications for both park management and managers of other populations. Within Yellowstone, it is important to have a better grasp of when and where pup fatalities are likely occurring by calculating weekly pup high counts. This may help managers and biologists more accurately pinpoint causes of death, understand and visualize patterns in fatalities and survival, and inform future population projections. Specifically, analyzing survival at a fine scale can provide more details and information for developing stage-structured population models and matrices, including more comprehensive survival and, potentially, harvest trends. Since several packs residing within Yellowstone straddle park boundaries, detailed survival and mortality information is crucial to understanding past and potential impacts of harvest. For example, parent or helper fatalities may influence the care of pups, or result in pack member turnover (Bassing et al. 2018), potentially reducing pup fitness or survival. This concept may apply to interagency management of Yellowstone wolves but may also be transferable to other populations. Finally, this information can serve as a basis for specifically analyzing what factors influence pup survival (i.e. prey availability, disease, etc.)

Future Work

Since this study only covered 2 years, analyzing more data, more packs, and across a broader timescale will be helpful for comparing survival rates and depicting survival trends. Analyzing high counts on an even finer scale (i.e. a 3-day scale) may improve detection probability analyses and more precisely locate specific fatality events. Finally, building a den presence analysis may better help explain differences in pup survival.

ACKNOWLEDGMENTS

I thank R. McIntyre for providing field notes used in data quantification, M. Hebblewhite for his contributions as my faculty adviser, B. Cassidy, C. Bishop, and M. Mitchell for their expertise, suggestions, and contributions to this project as committee members, and D. Smith and Yellowstone Wolf Project Staff for otherwise critical data and information.

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FIGURES

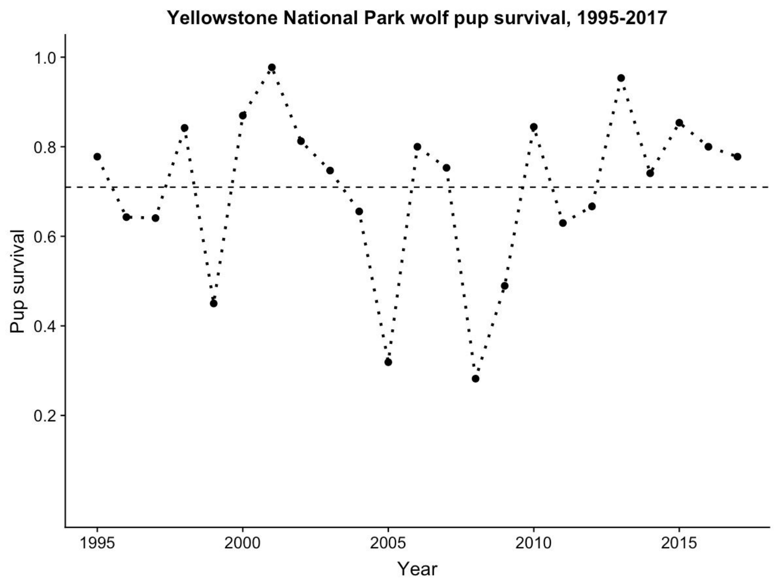

Figure 1. Wolf pup survival in Yellowstone National park by year from 1995 through 2017 (M. Metz personal communication).

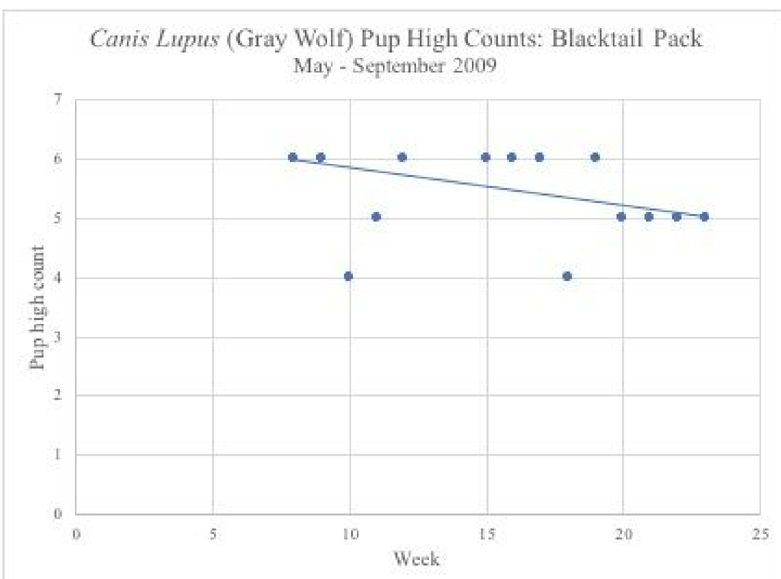

Figure 2. 2009 Blacktail Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

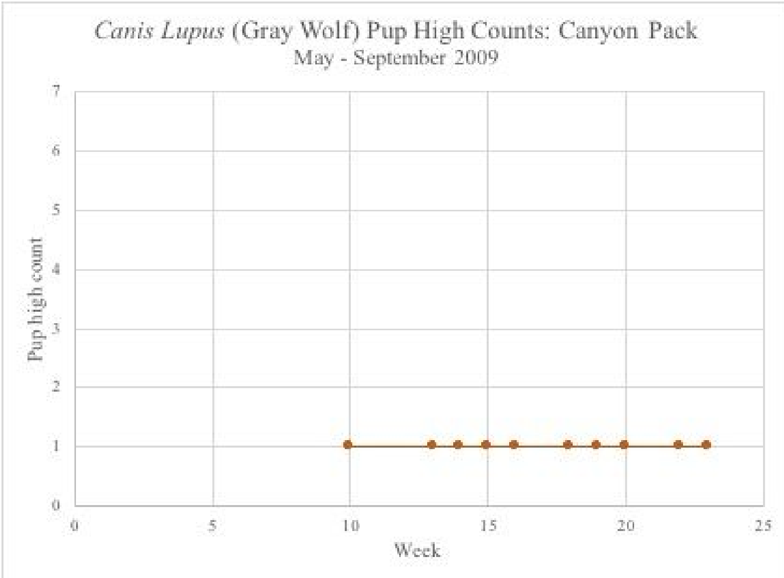

Figure 3. 2009 Canyon Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

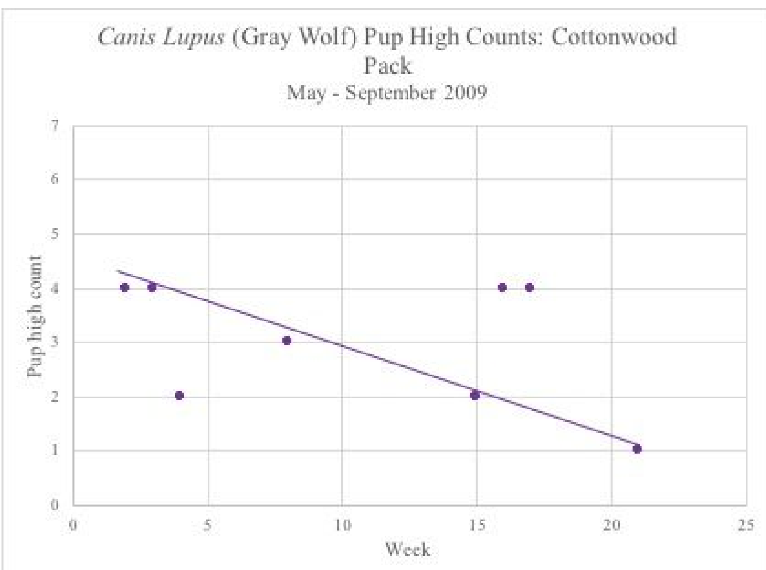

Figure 4. 2009 Cottonwood Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

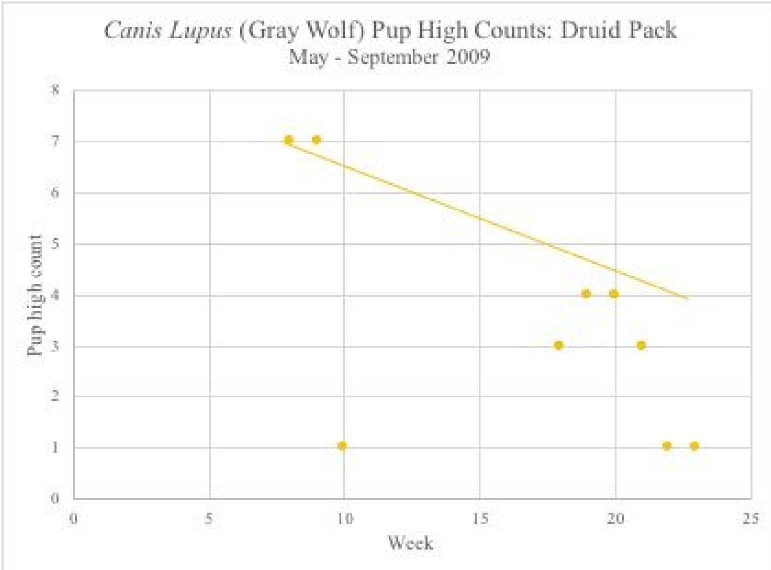

Figure 5. 2009 Druid Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

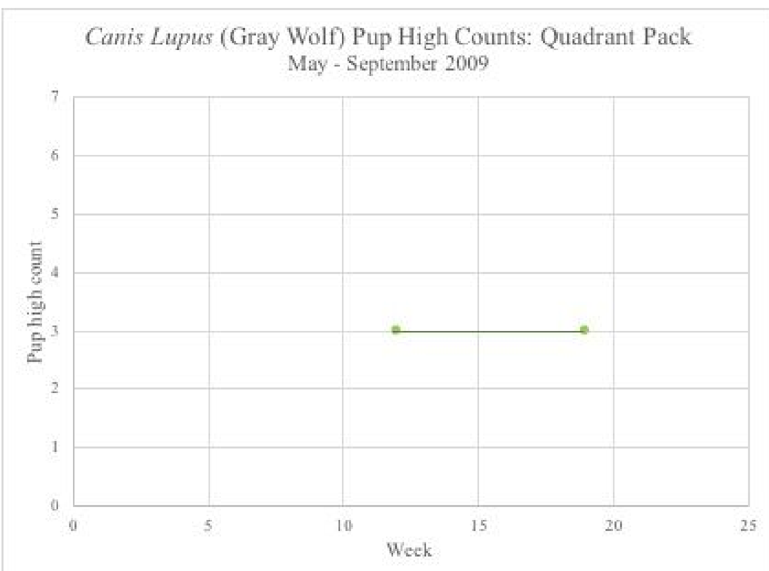

Figure 6. 2009 Quadrant Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

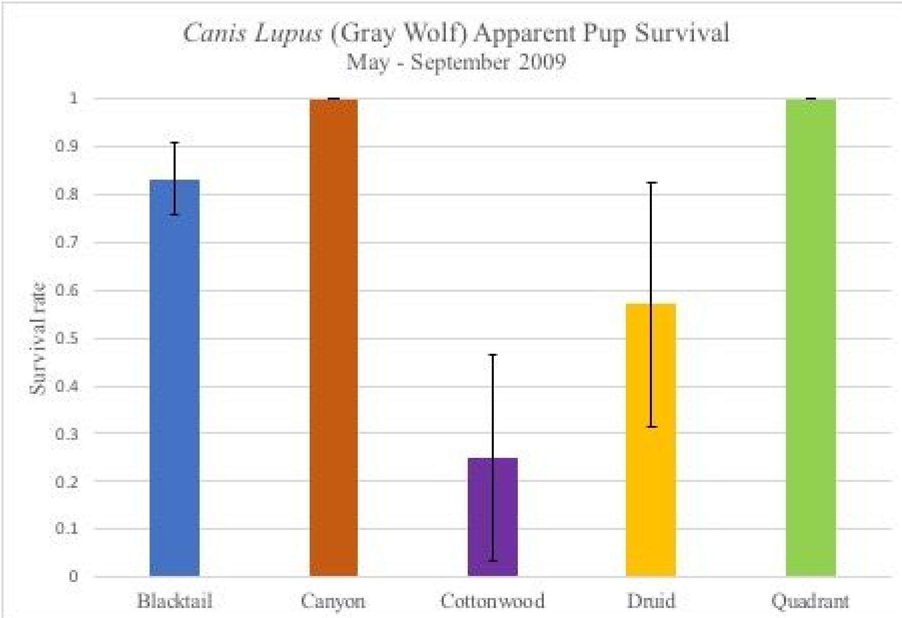

Figure 7. 2009 apparent pup survival by pack. Error bars calculated using standard error derived from high counts of total observations for each pack.

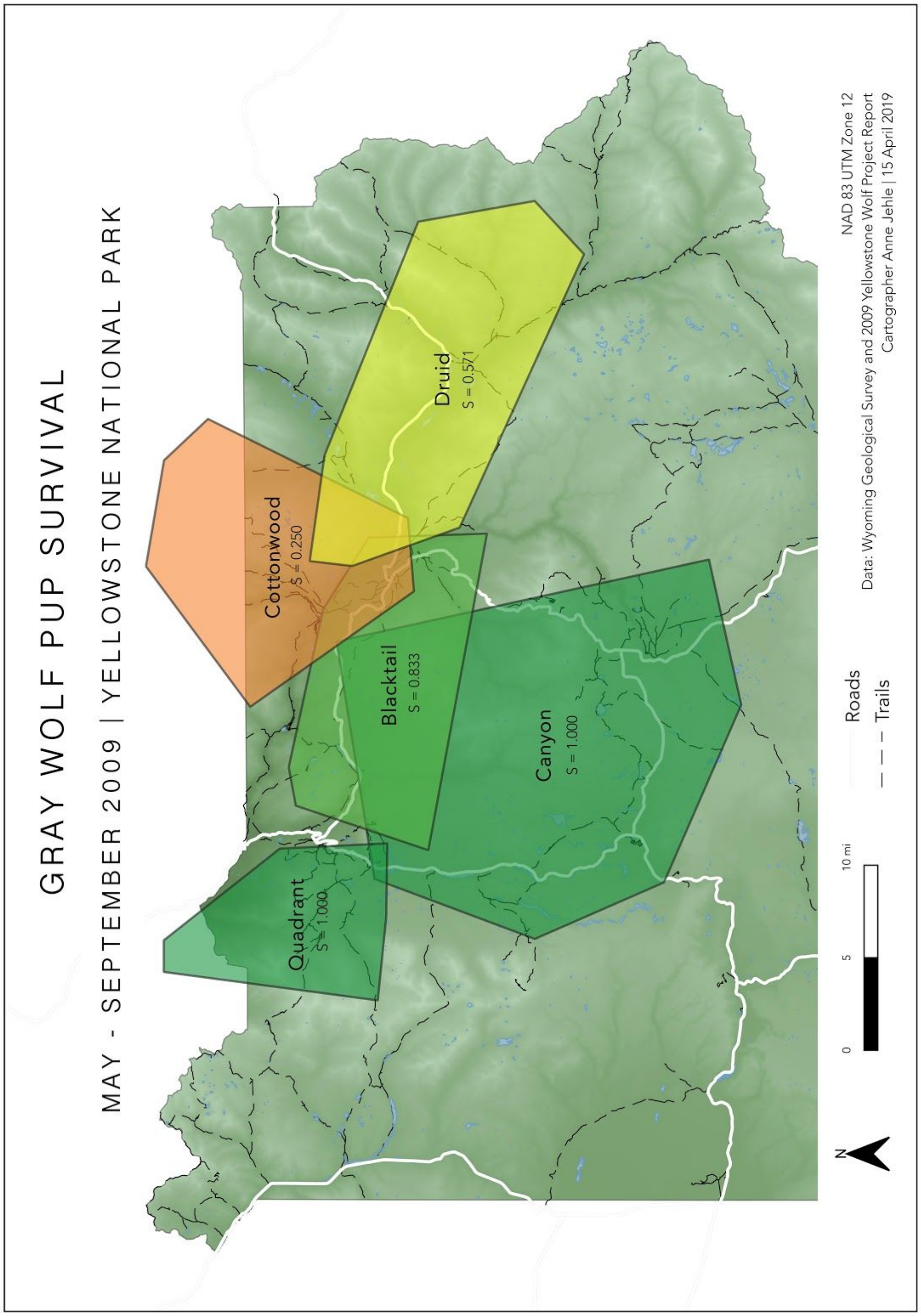

Figure 8. 2009 apparent pup survival represented by pack territory. Apparent survival (S) is designated below each pack name.

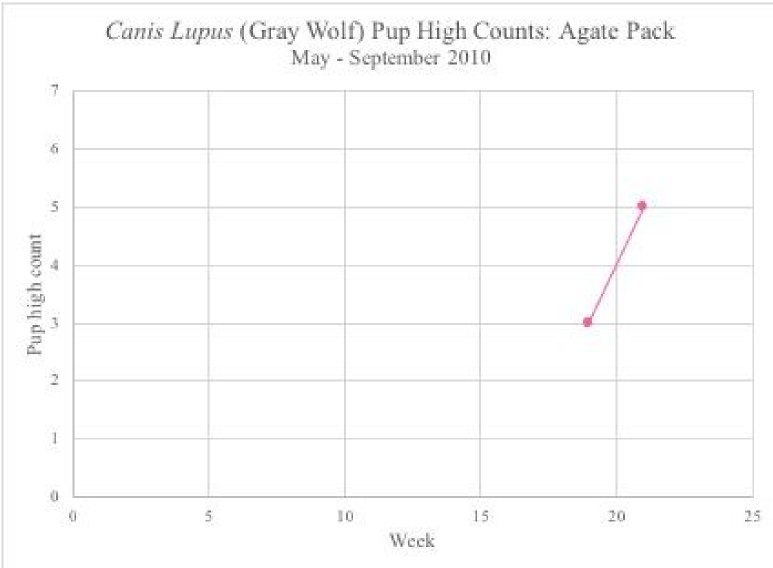

Figure 9. 2010 Agate Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

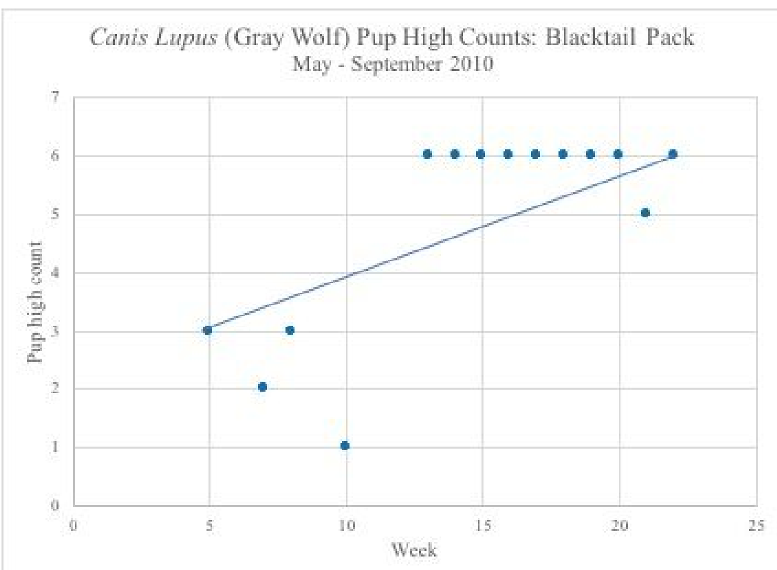

Figure 10. 2010 Blacktail Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

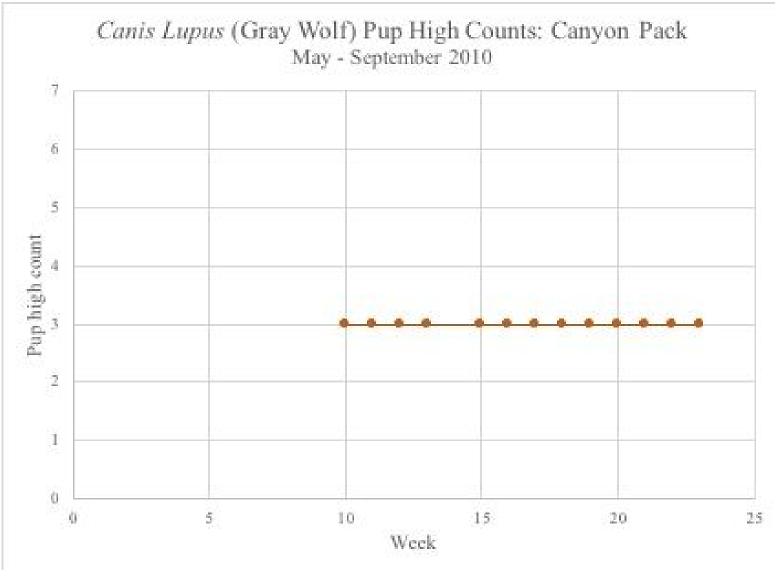

Figure 11. 2010 Canyon Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

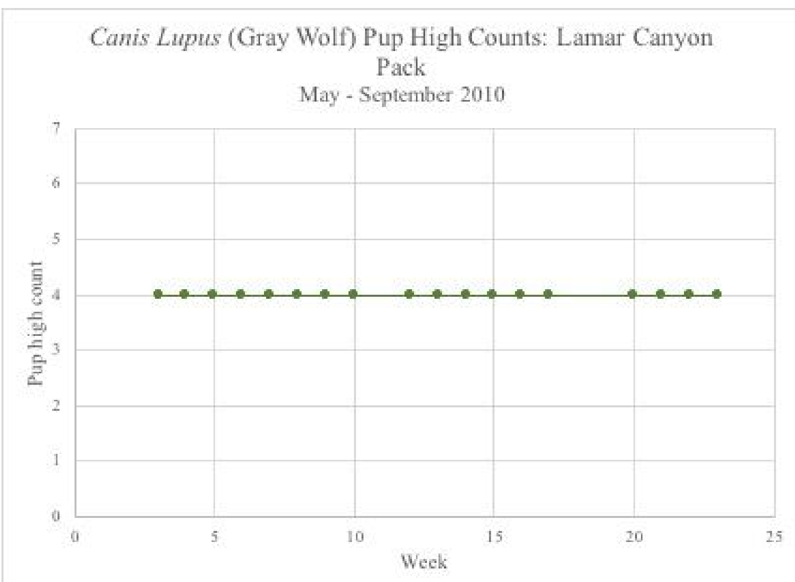

Figure 12. 2010 Lamar Canyon Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

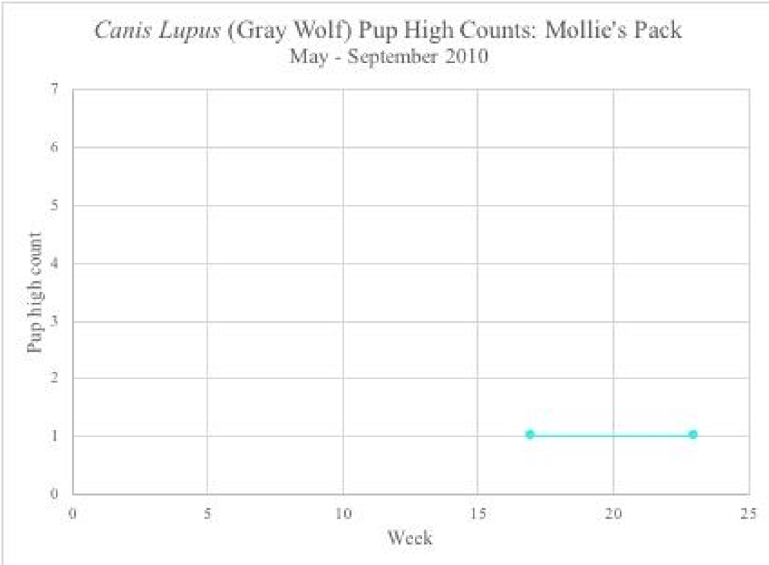

Figure 13. 2010 Mollie's Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

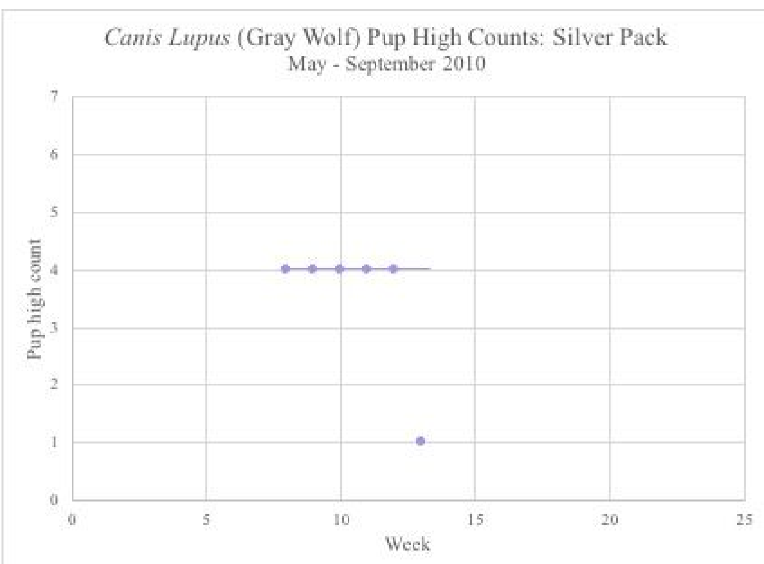

Figure 14. 2010 Silver Pack weekly pup high counts. Weekly high counts are represented by individual data points. Trendline represents difference between initial and final high counts.

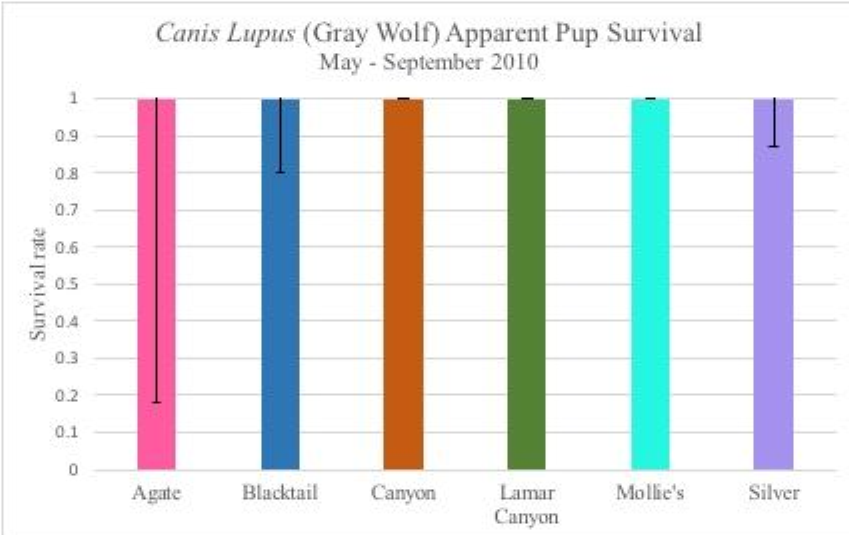

Figure 15. 2010 apparent pup survival by pack. Error bars calculated using standard error derived from high counts of total observations for each pack.

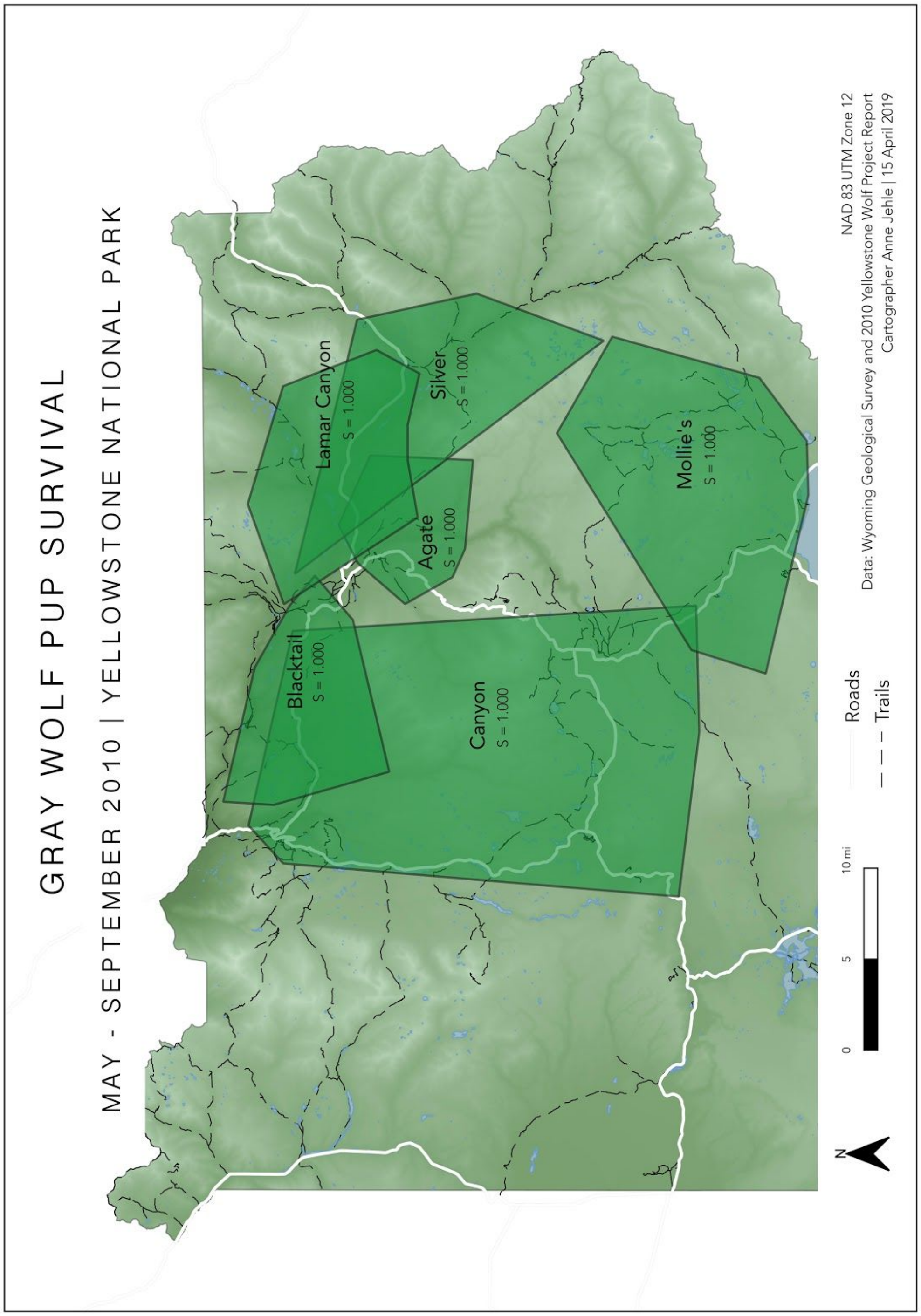

Figure 16. 2010 apparent pup survival represented by pack territory. Apparent survival (S) is designated below each pack name.