Northern Michigan University
NMU Commons

All NMU Master's Theses | Student Works

12-2016

Wolf Predation: Where and How Wolves Kill Beavers, and Confronting the Biases in Scat-Based Diet Studies

Thomas Gable
Northern Michigan University, thomasd.gable@gmail.com

Follow this and additional works at: https://commons.nmu.edu/theses

Part of the Zoology Commons

Recommended Citation

Gable, Thomas, "Wolf Predation: Where and How Wolves Kill Beavers, and Confronting the Biases in Scat-Based Diet Studies" (2016). *All NMU Master's Theses*. 122.
https://commons.nmu.edu/theses/122

This Open Access is brought to you for free and open access by the Student Works at NMU Commons. It has been accepted for inclusion in All NMU Master's Theses by an authorized administrator of NMU Commons. For more information, please contact kmcdonou@nmu.edu,bsarjean@nmu.edu.

WOLF PREDATION: WHERE AND HOW WOLVES KILL BEAVERS, AND CONFRONTING THE BIASES IN SCAT-BASED DIET STUDIES

By

Thomas D. Gable

THESIS

Submitted to
Northern Michigan University
In partial fulfillment of the requirements
For the degree of

MASTER OF SCIENCE

Office of Graduate Education and Research

December 2016

SIGNATURE APPROVAL FORM

Wolf Predation: Where and How Wolves Kill Beavers, and Confronting the Biases in Scat-Based Diet Studies

This thesis by Thomas D. Gable is recommended for approval by the student's Thesis Committee and Department Head in the Department of Biology and by the Assistant Provost of Graduate Education and Research.

____

Committee Chair: Dr. John Bruggink Date

____

First Reader: Dr. Steve Windels Date

____

Second Reader: Dr. Pat Brown Date

____

Department Head: Dr. John Rebers Date

____

Dr. Robert J. Winn Date
Interim Assistant Provost of Graduate Education and Research

ABSTRACT

WOLF PREDATION: WHERE AND HOW WOLVES KILL BEAVERS, AND CONFRONTING THE BIASES IN SCAT-BASED DIET STUDIES

By

Thomas D. Gable

Beavers can be a significant prey item for wolves in boreal systems but how wolves hunt beavers is largely unknown. I inferred how wolves hunt beavers by identifying 22 kill sites using clusters of locations from GPS-collared wolves in Voyageurs National Park, Minnesota. Where wolves killed beavers varied seasonally with the majority (58%) of kills in the spring occurring below dams and on shorelines while the majority (80%) of kills in the fall were near feeding trails and canals. I deduced that the typical hunting strategy has 3 components: 1) waiting near areas of high beaver use until a beaver comes near or on shore, 2) using concealment, and 3) immediately attacking the beaver, or ambushing the beaver by cutting off access to water.

Wolf diet is commonly estimated via scat analysis, and several studies have concluded that scat collection method can bias diet estimates. I tested whether different scat collection methods yield different diet estimates after accounting for other biases. I collected scats (2,406 scats) monthly from 4 packs via 3 scat collection methods in the Voyageurs National Park, Minnesota area, during April 2015–October 2015. Scat collection method did not yield different diet estimates but I did document temporal, inter-pack, and age class variability in diet estimates. To better estimate wolf population diets, researchers should collect ≥10–20 adult scats/pack/month from homesites and/or opportunistically from packs that are representative of the population of interest.

Copyright by

THOMAS D. GABLE

2016

DEDICATION

To my parents, Dan and Kay Gable, who have continually encouraged, loved, and supported me throughout my life.

ACKNOWLEDGMENTS

I first and foremost thank my parents, Dan and Kay Gable, who have always encouraged me to chase after my passions. My father introduced me to wild places when I was young and instilled in me a wonder of the natural world. I am forever grateful for that. My mother has continuously supported me, and over the past few years, brightened my days with warm phone calls, unexpected letters, and at times much appreciated care packages filled with baked goods! Thanks to my sisters, Jess and Anna Gable, for your joy, humor, and love. To my grandparents, Don and Vi Gable, and Harvey and Lynn Barkley, thank you for your continued support and interest in my life. A big thanks to all of my extended family on both the Gable and Barkley side.

Austin Homkes, I do not have words to express my thanks for all of the time, and effort you volunteered. Your >1,000 hr of fieldwork were an integral part to making this project a success, and your knowledge of the woods and keen eye were a key part in finding many kill sites. I feel lucky to have spent spring through fall exploring the Northwoods and chasing wolves with one of my closest friends.

Sean Johnson-Bice, thanks for all your time and effort, especially in “The Shack” – no one can bag ‘em like you can (125 scats in an afternoon)! Roberta Ryan, you were an immense help during August–October, and I am grateful for all of the time and effort you volunteered. Many thanks to Bryce Olson who provided logistical support and at times assisted with various aspects of the fieldwork for this project.

I feel indebted to John Stephenson at Grand Teton National Park for selecting me for my first field technician position. I was wholly unqualified for the position at the time. Nonetheless, you gave me a chance and I believe that position was a catalyst to get me where I am today. Many thanks!

A special thanks to Dr. Shannon Barber-Meyer for all of her help with wolf scat analysis. I really appreciate all of the time you took to both show me the 'process', and answer any questions I might have. You were a huge help! Thanks to Dr. L. David Mech for reviewing my first chapter and providing helpful suggestions. Thanks to Drs. K. Greg Murray and Kathy Winnett-Murray for your mentorship, advice, and friendship over the past several years.

Thank you to my advisors Drs. John Bruggink and Steve Windels. It has been a pleasure working with both of you for the duration of this project. Your guidance throughout my project was invaluable, and I have learned much from both of you. Thank you to Pat Brown for serving on my committee and providing helpful feedback on my thesis.

Lastly, I would like to thank God for the opportunities I have had and the people He has placed in my life.

Funding was provided by Voyageurs National Park, National Park Service Great Lakes Research and Education Center, Northern Michigan University, Rainy Lake Conservancy, Wolf Park, and 58 individuals via a crowd-funding campaign.

The first chapter of my thesis follows the format and style guidelines of PLoS ONE (http://journals.plos.org/plosone/s/submission-guidelines) while my second chapter follows the format and style guidelines of the Canadian Journal of Zoology (http://www.nrcresearchpress.com/page/cjz/authors).

TABLE OF CONTENTS

List of Tables....................vii

List of Figures....................viii

Chapter One: Where and How Wolves Kill Beavers....................1

Introduction....................1

Materials and Methods....................2

Results....................4

Discussion....................8

Literature Cited....................13

Chapter Two: Confronting the Biases in Wolf Diet Studies: Setting a Higher Standard..18

Introduction....................18

Study Area....................19

Materials and Methods....................20

Results....................25

Discussion....................26

References……....................32

Appendix A....................48

Appendix B....................69

Appendix C....................71

LIST OF TABLES

Table 2.1: Statistical comparisons used to identify the biases in wolf (*Canis lupus*) diet estimates from 4 wolf packs in and adjacent to Voyageurs National Park, MN during April–October 2015..39

Table 2.2: Number of adult wolf (*Canis lupus*) and pup scats from 3 different collection methods (GPS-clusters, homesites, and opportunistic) from 4 wolf packs in and adjacent to Voyageurs National Park, MN during April–October 2015..40

LIST OF FIGURES

Figure 1.1: Examples of evidence found at beaver kill sites (A,B,C), and of wolf behavior when in active beaver habitats (D) in Voyageurs National Park 2015.............................41

Figure 1.2: Locations (solid circles) and path (line) from a GPS-collared wolf (4–hr fix interval) in Voyageurs National Park during April–May 2015 when A) at Beaver Kill Site 2 and B) when bedded next to a small channel below an active beaver dam (Map data: Google, DigitalGlobe)...42

Figure 2.1: Rarefactions curves examining the impact of scat sample size on 2015 monthly (April–October) wolf (*Canis lupus*) pack diet diversity in Voyageurs National Park, Minnesota...43

Figure 2.2: Estimated diet of 3 wolf (*Canis lupus*) packs–Ash River Pack (A), Moose River Pack (B), Sheep Ranch Pack (C)–and the population (D) in and adjacent to Voyageurs National Park based on 3 scat collection methods (clusters, homesites, and opportunistic) during the 2015 denning season (April–August) 44

Figure 2.3: Estimated diet of 2 wolf (*Canis lupus*) packs–Ash River Pack (A), Moose River Pack (B)–and the population (C) in and adjacent to Voyageurs National Park based on 2 scat collection methods (at clusters and opportunistically) during the 2015 ice-free season (April–October)... 45

Figure 2.4: Comparison between adult and pup wolf (*Canis lupus*) diet (A) for the Ash River and Moose River packs from May–August 2015...46

Figure 2.5: Inter-pack (A) and monthly (B) variability in wolf (*Canis lupus*) diet in and adjacent to Voyageurs National Park from April 2015–October 2015.............................47

CHAPTER ONE

WHERE AND HOW WOLVES KILL BEAVERS

Introduction

Wolves (*Canis lupus*) primarily prey upon large ungulate species [1]. However, they are opportunistic hunters and use alternative prey species seasonally when they are abundant, vulnerable, and easy to capture [2–5]. Wolves and beavers co-occur throughout the boreal ecosystem, and wolves can be significant predators of beavers [6,7]. During winter, beavers are usually in their lodges or foraging below the ice and thus are seldom available to wolves [8]. From ice-out in spring through freeze up in late fall beavers must forage on land to increase fat reserves and to re-supply food caches to survive the upcoming winter [9,10]. Consequently, wolf predation of beavers is highest during this period of vulnerability, and beavers can be important prey for wolves [11–13]. Indeed, wolves have used beaver as a secondary or tertiary prey item in many areas [2,14–17]. In some systems under certain conditions, such as high beaver densities or low ungulate densities, beavers can actually be the primary summer prey of wolves [6,13,18].

Despite this, little is known about wolf-beaver interactions in systems where the species co-occur. In particular, the manner in which wolves hunt, attack, and capture beavers is unknown. In a comprehensive review of wolf hunting behavior, Mech et al. [19:146] concluded that there were “no actual descriptions of wolves hunting beavers”. The lack of observations is not surprising as riparian vegetation is often dense around active beaver habitats during the ice-free season, and in winter beavers spend most of their time below the ice where they are safe. Thus other methods must be used to understand how wolves hunt beavers.

A common method to understand wolf predation on ungulates is to document kill sites by searching areas where there were clusters of locations from GPS-collared wolves [20–22]. However, finding kill sites of small prey species is difficult because wolves can consume the entire carcass in a short period [23–25]. Nonetheless, some studies have successfully documented beaver kill sites at clusters [20, 21, 25, 26]. Thus, I sought to infer wolf hunting behavior from beaver kill sites to understand how and where wolves hunt beavers.

Materials and Methods

Study Area

Voyageurs National Park (VNP) is located in northern Minnesota (USA) along the Ontario (Canada) border (48°30' N, 93°00' W). Voyageurs National Park is an 882 km^2 landscape dominated by forests and lakes, with nearly 50% of the park comprised of aquatic habitat types [27]. Four large lakes cover 342 km^2 (39%) of the park, and 26 smaller lakes are scattered throughout the landmasses of the park. Beaver impoundments are abundant throughout the park as the park has sustained high beaver densities for over 40 yr [28,29]. Voyageurs National Park is in the Laurentian Mixed Forest Province, which is a transition zone between the southern boreal forest and northern hardwood forest [30]. As a result, the park is a mosaic of deciduous and coniferous forests. Lakes freeze during late October to mid-November with ice-out occurring during late April to early May [31].

White-tailed deer (*Odocoileus virginianus*) are common in VNP while moose (*Alces americanus*) are relatively rare [32]. Wolf densities in the area are high (4–6 wolves/100 km^2), and the average home-range size in 2015 was 115.8 km^2 (VNP, unpublished data). Hunting and trapping are not allowed in the park. Recreational trapping of beavers outside the park is common. Wolf hunting and trapping are illegal in Minnesota at present but are legal in Ontario.

Wolf Capture and Collaring

I captured wolves from 4 packs during 2012–2015 using #7 EZ Grip foothold traps (Livestock Protection Company, Alpine, Texas). Wolves were immobilized with 10 mg/kg ketamine and 2 mg/kg xylazine using a syringe pole. Once immobilized, I fitted wolves with global positioning system (GPS) telemetry collars (Lotek IridiumTrackM 1D or 2D, Lotek Wireless Inc, Newmarket, Ontario, Canada; Vectronic Vertex Survey, Vectronic Aerospace, Berlin, Germany). Morphological measurements, tissue samples, and blood were collected. Sex and age were also recorded. I reversed wolves with 0.15 mg/kg of yohimbine and monitored through recovery. GPS-collar fix intervals were set to 20 minutes, 4 hours, 6 hours or 12 hours, depending on the collar type, where the pack was located, and whether there was > 1 collar in the pack at that time. Locations were uploaded (12 locations/upload) every 4 hours to 6 days depending on the fix interval. All capture and handling of wolves was approved by the National Park Service's Institutional Animal Care and Use Committee and conducted in accordance with American Society of Mammalogists Guidelines for use and handling of wildlife mammals for research [33].

Clusters and Identifying Kill Sites

From April 2015 to November 2015 I examined localized clusters of wolf activity to document kill sites. Potential kill sites were determined by identifying clusters of locations from GPS-collared wolves using ArcGIS 10.2 [34]. Clusters were defined as consecutive locations within a 200 m area for ≥ 4 hours [35]. I examined clusters 1–28 days ($\bar{X}$ = 10 days) after the wolf or wolves were present. Once at clusters I systematically searched for prey remains. When kill sites were found, prey remains were collected, the location of the kill was recorded, and photographs were taken to document the site. I recorded all wolf and beaver sign at kill sites as well as evidence of a struggle such as drag marks, depressed vegetation, and blood trails. I estimated carcass utilization to the nearest 5%, with 99% representing the greatest carcass utilization still detectable. I estimated the distance of the kill site to the nearest body of water (lake, pond, river, or stream) by examining May 2015 aerial imagery in Google Earth Pro 7.1.4 [36].

Collared wolves were assumed to be alone at kill sites if: 1) all beaver remains found were at the site or at GPS locations, and 2) there was only 1 wolf bed at the site, or all wolf beds at the site were associated with GPS locations [25]. I determined the minimum time a collared wolf was at a kill site based on the time between the first and last location at the site. Maximum time spent at a kill site was determined by taking into account the fix interval prior to and after the first and last locations respectively (e.g., if minimum time spent was 8 hr and the fix interval was 4 hr, then the maximum time spent at the kill site was 16 hr). Due to the large fix intervals, these numbers provide the range of time wolves spent at kill sites. Thus I calculated the estimated time spent at kill sites as the means of the minimum and maximum times spent at kill sites.

Results

I documented 22 beaver kill sites from 2 April 2015 to 5 November 2015. Of those, 12 were in spring (2 April 2 – 29 May) and 10 in fall (20 September – 4 November). I found 4 kill sites from GPS collars with 20-min fix intervals, 7 from GPS collars with 4-hr fix intervals, 9 from GPS collars with 6-hr fix intervals, 1 from GPS collars with 12-hr fix intervals, and 1 kill site was found opportunistically. I concluded that collared wolves were alone at 16 (73%) kill sites, with other wolves at 4 (18%) sites, and are uncertain about the remaining 2 sites.

Kill sites were typified by a disturbed area with beaver remains such as fur, stomach contents, bone fragments, castor glands, skull remnants, or any combination of those present (Fig 1.1). Generally, beaver kill sites were difficult to detect as mean carcass utilization was 98% (range: 85–100%). I was able to recover the lower mandible, skull, or teeth at 7 (32%) kill sites. At most of kill sites, all remains were located where the beaver appeared to have been killed. However, at some sites remains (often the skull) were found up to 180 m away. The mean minimum time wolves spent at kill sites was 10.6 ± 8.0 hr (range: 4.0–30.0), the mean estimated time spent, 15.4 ± 9.2 hr (range: 5.7–36.0), and the mean maximum time spent, 20.2 ± 11.1 hr (range: 6.0–48.0).

Kill sites ranged from 1 to 222 m from water ($\bar{X}$ = 24.5 ± 48.5 m) from water, and all but 2 sites were < 27 m from water. With the 2 farthest distances (99 m and 222 m) excluded, the mean distance from water was 10.9 ± 7.5 m. Based on physical evidence, wolves appeared to have attacked beavers in the water and pulled them out at 6 (27%) kill sites.

I classified kill sites into 8 categories based on the location of the kill site and my interpretation of how wolves killed the beaver. I documented seasonal variation in kill site type and frequency. Kill sites below the dam and on shore composed 50% of all spring kill sites, whereas kill sites near feeding trails and feeding canals composed 80% of all fall kill sites. Descriptions individual kill sites can be found in Appendix A.

At Dams

I identified 1 kill site where a wolf killed a kit beaver while on a small point 5 m from a small beaver dam. The matted vegetation suggested the wolf pulled the kit out of the water while on the end of the point, but it is possible that the wolf was in the water when it attacked the beaver (Fig 1.1).

At Lodges

In spring, water levels in VNP can be > 1 m lower than during the previous fall. As a result many shoreline beaver lodges are left completely out of the water in spring until water levels increase [37]. Thus, beavers must travel over land (up to 100 m) exposed to predators to reach open water. I documented 1 kill site that occurred 10 m from a lodge that had no open water nearby. I postulate that the wolf waited outside the lodge until a beaver exited the lodge heading for open water. Based on trampled vegetation and drag marks, it appears that the wolf caught the beaver immediately once the beaver left the lodge (drag marks started 1 m from lodge). The wolf then dragged the beaver 10 m behind the lodge where the wolf ate the beaver.

Below Dams

I identified 4 kill sites below beaver dams. In 2 instances beavers were in the small channels below the dam when, based on the matted vegetation, they appeared to have been attacked in the water, pulled out, and killed nearby. The kill sites were 28 and 33 m downstream from the dams. In the other 2 instances, the beavers were on land when attacked; these kill sites were much closer to the dams (8 and 10 m; Figs 1.1 and 1.2).

Feeding Canals

I documented 2 kill sites where a wolf or wolves appeared to have attacked and pulled beavers out of feeding canals. In both instances, the feeding canals were at least 1 m deep and 1 m wide, and there was trampled vegetation leading from the canals to the kill sites. The beavers were consumed < 5 m from the feeding canals.

Feeding Trails

I documented 8 kills that occurred on or near feeding trails. With the exception of 1 kill site that was 99 m from water, kill sites on feeding trails were 5.1–23.1 m from water ($\bar{X}$ = 13.3 ± 5.9 m).

Near Shores

I documented 3 kill sites near or on the shoreline of a lake or river. These kill sites were not near any feeding trails, and there was no evidence of fresh cuttings nearby. All 3 sites were < 200 m from active lodges so the beavers killed at these sites probably were not dispersing. The collar locations at the sites did not help clarify what occurred due to the relatively long (4–6 hr) fix intervals.

Small Waterways

I identified 2 kill sites where, based on matted vegetation and drag marks, wolves appeared to have attacked and pulled beavers out of small waterways. Beavers used these waterways to travel between bodies of water and both sites were >200 m from the nearest known lodge. Although kill sites along small waterways are similar to kill sites at feeding canals, they differ in that beavers traveling in feeding canals are moving from water to land to forage whereas in small waterways beavers are traveling between bodies of water.

Forest Interior

I documented 1 instance of a wolf killing a beaver in a dense aspen stand 222 m from the nearest body of water. I found no evidence of fresh cuttings or beaver activity near the kill site. Thus, I assumed that this was a dispersing beaver traveling through the woods to reach a body of water when a wolf either opportunistically encountered and killed it, or scent-tracked it from the water.

Discussion

Fifty years ago, Mech [38:152] stated, "the manner in which wolves hunt beavers is unknown". Since then thousands of hours of wolf observations have occurred across the world, and still no observations of a wolf hunting a beaver exist [19]. Although there are limitations when inferring hunting behavior from kill sites, I think that the combination of physical evidence at kill sites and observations of wolf behavior based on clusters of GPS locations in active beaver habitats both where I found kill sites and where I did not provide a viable substitute to visual observations of predation behavior of wolves (Figs 1.1 and 1.2).

I documented more beaver kill sites (22) than previous studies by investigating areas where clusters of locations from GPS-collared wolves occurred. Short fix intervals ($\leq$ 30 min) have been thought necessary for identifying kill sites of small prey [25,26,39]. However, I found 17 (80%) of 22 kill sites using collars with fix intervals $\geq$ 4 hr. My success in finding these kill sites was in part a result of wolves spending relatively long periods ($\bar{X}$ = 15.4 hr) at kill sites.

Wolves appeared to have been alone at 73% of beaver kill sites, which is to be expected as wolves frequently travel alone from spring through early fall [24,25,40].

Beavers in VNP can exceed 20 kg and can be a substantial meal for a wolf [37]. Peterson and Ciucci [1] stated that a 20 kg beaver can be entirely consumed within a few hours, especially with multiple wolves present. Although wolves might consume a beaver quickly, my results suggest wolves remain at beaver kill sites for a substantial period regardless of whether alone (15.6 hr) or with others (15.0 hr). However, my estimates of time spent at kill sites might be positively biased because I would not have detected kill sites where wolves were present < 4 hr.

Where Wolves Kill Beavers

During spring, wolves appear to hunt and kill beavers at or near a variety of habitat features. In fall, beavers must travel on land more frequently to access, obtain, and transport food both to store in the cache and to consume [10,41]. Therefore it is not surprising that 80% (8/10) of kill sites in fall were at feeding canals or trails [6,8]. Mech et al. [19] postulated that wolves likely hunt beavers during the ice-free season by targeting beaver trails going inland. My results agree with this, though this strategy appears to be much more prevalent in fall than spring.

Mech and Peterson [42] and Peterson and Ciucci [1] speculated that wolves kill beavers near beaver dams based on the amount of time wolves and beavers spend near beaver dams. I confirmed this as 5 (23%) kills occurred at, or below, beaver dams. However, kill sites near dams were more prevalent in spring than fall, consistent with my observations that wolves spent a substantial period near active beaver dams in spring but not fall. I think that wolves might wait below dams because if a beaver was on the down slope of the dam it would be challenging for the beaver to turn around before it was attacked (see Kill Sites 2 and 13, Appendix A). Much of this is based on observations of clusters where wolves appeared to have bedded down < 3 m from small channels or beaver trails below dams for several hours but never made a kill (Fig 1.2).

How Wolves Hunt Beavers

I think a typical hunting strategy consists of 3 components: 1) waiting near areas of high beaver use (e.g., feeding trails) until the beaver comes near shore or ashore, 2) using vegetation or the dam for concealment, and 3) attacking the beaver by cutting off access to water, or immediately attacking the beaver (e.g. ambush). Wolves spend about $^{1}/_{3}$ of their lives hunting [19], and thus likely put themselves in the best position to encounter beavers when in active beaver habitats. Clusters of locations in active beaver habitats were typified by a wolf bedding down next to high beaver use areas such as small channels, feeding trails, dams and lodges (Figs 1.1 and 1.2). In some instances wolves bedded for several hours and then moved nearby to another area of beaver activity and bedded again.

Others have speculated that waiting near areas of beaver use would be a profitable strategy for wolves [1,19]. Thurber and Peterson [43] observed a lone wolf that they thought was actively hunting beavers during mid-winter thaws by bedding down next to beaver trails. Wolves appear to exhibit this ambushing behavior when hunting other prey species as well [44]. Mech [45] observed wolves waiting for 3 hr in a depression to ambush muskoxen (*Ovibos moschatus*)–even though the herd was only a few hundred meters away–and concluded that it appeared that the wolves chose the location to maximize their chance of success. Compared to ungulates, beavers have small home ranges and are very predictable, as they must eventually come on shore to forage or cross over their dams to reach another body of water. Thus, waiting concealed at these areas appears to be an effective strategy that is almost certainly used by wolves.

Once a wolf has located a beaver on or near land it either attacks the beaver by cutting off access to the water, or ambushing the beaver. At kill sites 7 and 14, fresh wolf tracks indicate wolves followed the shoreline to a feeding trail, then followed the feeding trail and killed a beaver < 20 m from water on that trail. Basey and Jenkins [46] thought that intercepting a beaver or cutting off its path to water was the most likely strategy for any predator hunting beavers. Similarly, Mech [47] suggested that wolves might follow shorelines until they find a beaver inland that they could easily subdue.

However, wolves also appear to use ambush as a strategy to hunt beavers. In such cases, wolves likely are not waiting for the beaver to move inland before attacking it (see kill sites #2, #5, #12, and #13, Appendix A). At 27% (6/22) of kill sites, wolves appeared to have attacked beavers in the water and then consumed them close by on shore. For this to happen, 1 of 3 sequences must have occurred: 1) the wolf attacked the beaver on land but the beaver was able to get back to the water where it was subsequently subdued, 2) the wolf waited by the water, determined it could successfully kill the beaver, and attacked the beaver in the water, or 3) the beaver reached the water after detecting the wolf but was intercepted by the wolf in the water. In 83% (5/6) of these kills, beavers were pulled from waterways or feeding canals that were both ≥ 1 m deep and wide. Given this, it would seem beavers would be able to avoid being captured once they reached the water (e.g., sequences 1 and 3). Indeed, I documented 1 instance where a beaver successfully escaped from a wolf in the water (see Appendix B). Therefore, sequence 2 appears to be the most plausible explanation for how wolves attacked beavers in the water and killed them on land. However, I do not know why a wolf would attack a beaver that was headed inland in the water, or conversely, wait for a beaver on land to return to water before attacking it. Nonetheless, I am confident that wolves do in fact attack beavers in the water, pull them out of the water, and then kill and consume them on shore.

Although wolves appear to use ambush as a hunting strategy, there is undoubtedly a certain level of opportunism that exists when wolves are traveling across the landscape [48]. However, without direct observation, I cannot say whether wolves waited for, searched for, or encountered beavers opportunistically at most kill sites because I do not know how long wolves were near kill sites prior to killing beavers.

The Key to Understanding Wolf-Beaver Dynamics?

I have provided the most thorough description of how and where wolves hunt beavers. However, there is still much to be learned about how wolves hunt beavers, and how wolf predation impacts beaver populations. To date, the impact of wolf predation on beaver populations has been estimated by: 1) calculating predation rate based on the wolf population, the beaver population, and the percent diet that is beaver (derived from scat analysis; [12]), 2) assuming a causal relationship between wolf removal and increases in beaver density [49], and 3) estimating the maximum possible predation rate for a growing beaver population [37]. By identifying kill sites, it is possible to calculate more accurate estimates of predation because most, if not all, of the beaver kills made by an individual wolf could be found. Other aspects of wolf-beaver dynamics could also be examined such as the impact of wolf predation on the demographic structure of beaver populations.

Thus, identifying kill sites might be the key to fully understanding this important, but poorly understood, predator-prey relationship in boreal ecosystems.

References

1. Peterson RO, Ciucci P. The wolf as a carnivore. In: Mech LD, Boitani L, editors. Wolves: behavior, ecology, and conservation. Chicago: University of Chicago Press. 2003. pp. 104-130.

2. Tremblay JP, Jolicoeur H, Lemieux R. Summer food habits of gray wolves in the boreal forest of the Lac Jacques-Cartier highlands, Québec. Alces 2001;37: 1–12.

3. Darimont CT, Reimchen TE. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. Can J Zoo. 2002;80: 1638–42.

4. Wiebe N, Samelius G, Alisauskas RT, Bantle JL, Bergman C, Carle R, et al. Foraging behaviours and diets of wolves in the Queen Maud Gulf Bird Sanctuary, Nunavut, Canada. Arctic. 2009;62: 399–404.

5. Nichols TC. Cooperative hunting of Canada geese (*Branta canadensis*) by gray wolves (*Canis lupus*) in northern Quebec. Can Field Nat. 2015;129: 290–92.

6. Hall AM. Ecology of beaver and selection of prey by wolves in central Ontario. M.Sc. Thesis, University of Toronto. 1971.

7. Baker BW, Hill EP. Beaver (*Castor canadensis*). In: Feldhammer G, Thomspon B, and Chapman J, editors. Wild mammals of North America biology, management, and conservation. Baltimore:John Hopkins University Press; 2014. pp. 288–310.

8. Shelton PC. Ecological studies of beavers, wolves, and moose in Isle Royale National Park, Michigan. Ph.D. Dissertation, Purdue University. 1966. Available: http://docs.lib.purdue.edu/dissertations/AAI6613260/.

9. Aleksiuk M, Cowan I. Aspects of seasonal energy expenditure in the beaver (*Castor canadensis* Kuhl) at the northern limit of its distribution. Can J Zoo.1969;47: 471–81.

10. Slough BG. Beaver food cache structure and utilization. J Wildl Manage. 1978;42: 644.

11. Fuller TK. Population dynamics of wolves in North-central Minnesota. Wildl Monogr. 1989;105: 3–41.

12. Romanski MC. Estimates of abundance and predation - the population ecology of beaver in Isle Royale National Park. M.Sc. Thesis, Michigan Technological University, 2010. Available: https://irma.nps.gov/DataStore/DownloadFile/427062.

13. Latham ADM, Latham MC, Knopff KH, Hebblewhite M, Boutin, S. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. Ecography. 2013;36: 1276–90.

14. Peterson RO. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph Series. 11:1-210. 1977.

15. Messier F, Crête M. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia. 1985;65: 503–12.

16. Peterson RO, Page RE. The rise and fall of Isle Royale wolves, 1975-1986. J Mamm. 1988;69: 89–99.

17. Forbes GJ, Theberge JB. Response by wolves to prey variation in central Ontario. Can J Zoo. 1996;74: 1511–20.

18. Voigt DR, Kolenosky GB, Pimlott DH. Changes in summer foods of wolves in central Ontario. J Wildl Manage. 1976;40: 663–68.

19. Mech, LD, Smith DW, MacNulty DR. Wolves on the hunt: the behavior of wolves

hunting wild prey. Chicago: University of Chicago Press. 2015.

20. Zimmermann B, Wabakken P, Sand H, Pedersen HC, Liberg O. Wolf movement patterns: a key to estimation of kill rate? J Wildl Manage. 2007;71: 1177–82.

21. Sand H, Wabakken P, Zimmermann B, Johansson Ö, Pedersen HC, Liberg O. Summer kill rates and predation pattern in a wolf–moose system: can we rely on winter estimates? Oecologia. 2008;156: 53–64.

22. Morehouse AT, Boyce MS. From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape. Front Ecol Environ. 2011;9: 440–45.

23. Franke A, Caelli T, Kuzyk G, Hudson RJ. Prediction of wolf (*Canis lupus*) kill-sites using hidden Markov models. Ecol Model. 2006;197: 237–46.

24. Demma DJ, Barber-Meyer SM, Mech LD. Testing global positioning system telemetry to study wolf predation on deer fawns. J Wildl Manage. 2007;71: 2767–75.

25. Palacios V, Mech LD. Problems with studying wolf predation on small prey in summer via global positioning system collars. Euro J Wildl Res. 2010;57: 149–56.

26. Sand H, Zimmermann B, Wabakken P, Andrèn H, Pedersen HC. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf‐ungulate ecosystems. Wildl Soc Bull. 2005;33: 914–25.

27. Hop K, Faber-Langendoen D, Lew-Smith M, Aaseng N, Lubinski, S. Final Report, USGS-NPS vegetation mapping program, Voyageurs National Park, Minnesota. U.S. Geological Survey, La Crosse, Wisconsin. 2001.

28. Johnston CA, Naiman RJ. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landsc Ecol. 1990;4: 5–19.

29. Johnston CA, Windels, SK. Using beaver works to estimate colony activity in boreal

landscapes. J Wildl Manage. 2015;79: 1072–80.

30. Bailey RG. 1980. Description of the ecoregions of the United States. United States Department of Agriculture. Miscellaneous Publication No. 1391.

31. Kallemeyn, LW, Holmberg KL, Perry JA, Odde BY. Aquatic synthesis for Voyageurs National Park. U.S. Geological Survey, Information and Technology Report 2003-0001. 2003.

32. Windels SK, Olson BT. 2015 Voyageurs National Park Moose Population Survey Report. Natural Resource Data Series NPS/VOYA/NRDS—2015/XXX. National Park Service, Fort Collins, Colorado. 2015.

33. Sikes RS. et al. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J Mamm. 2016;92: 235–53.

34. ESRI. ArcMap GIS. Ver. 10.2. Environmental System Research Institute, Inc. Redlands, California. 2015.

35. Latham ADM. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta. Ph.D. Dissertation, University of Alberta, 2009.

36. Google. Google Earth Pro. Ver. 7.1.4. Google, Mountain View, California. 2015.

37. Smith DW, Peterson RO. Effects of regulated lake levels on beavers in Voyageurs National Park, Minnesota. Midwest Regional Office, Omaha, Nebraska 68102. 1988.

38. Mech LD. The wolves of Isle Royale. National Park Service Fauna Series. 7:1-210. 1966. Available: https://archive.org/details/wolvesofisleroya00royal.

39. Webb NF, Hebblewhite M, Merrill EH. Statistical methods for identifying wolf kill sites using global positioning system locations. J Wildl Manage. 2008;72: 798–807.

40. Barber-Meyer S, Mech LD. Gray wolf (*Canis lupus*) dyad monthly association rates by demographic group. Can Wildl Bio Manage. 2015;4: 163–68.

41. Buech RR. Sex differences in behavior of beavers living in near-boreal lake habitat. Can J Zoo 1995;73: 2133–43.

42. Mech LD, Peterson RO. Wolf-prey relations. In: Mech LD, Boitani L, editors. Wolves: behavior, ecology, and conservation. Chicago: University of Chicago Press. 2003. pp. 131-160.

43. Thurber JM, Peterson RO. Effects of population density and pack size on the foraging ecology of gray wolves. J Mamm. 1993;74: 879–89.

44. Haber GC. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. Dissertation, University of British Columbia. 1977. Available: https://open.library.ubc.ca/cIRcle/collections/ubctheses/831/items/1.0094168.

45. Mech LD. Possible use of foresight, understanding, and planning by wolves hunting muskoxen. Arctic 2007;60: 145–49.

46. Basey JM, Jenkins SH. Influences of predation risk and energy maximization on food selection by beavers (*Castor canadensis*). Can J Zoo. 1995;73: 2197–208.

47. Mech LD. The wolf: the ecology and behavior of an endangered species. Garden City: The Natural History Press. 1970.

48. Huggard DJ. Prey selectivity of wolves in Banff National Park. Ph.D. Dissertation, University of British Columbia. 1991. Available: https://open.library.ubc.ca/cIRcle/collections/ubctheses/831/items/1.0098434.

49. Potvin F, Breton L, Pilon C. Impact of an experimental wolf reduction on beaver in Papineau-Labelle Reserve, Quebec. Can J Zoo 1992;70: 180–83.

CHAPTER TWO

CONFRONTING THE BIASES IN WOLF DIET STUDIES: SETTING A HIGHER STANDARD

Introduction

"Carefully correcting for biases inherent in indirect methods of diet determination has a profound effect on the assessment of diet composition and the estimated number of prey animals killed by a carnivore population." – Wachter et al. 2012

Estimating the diet of carnivores is important for understanding predator behavior and ecology, including predator-prey relationships, disease transmission, and energetics. Carnivore diets are most commonly determined by collecting scats and identifying the prey remains present (Klare et al. 2011). The assumption when estimating diet via scat analysis is that the scats collected are representative of all the scats deposited for a particular population (Steenweg et al. 2015). When this assumption is violated, diet estimates are biased to some, often unknown, degree. Because diet estimates from scat analysis are indirect, bias will always be present to some degree. However, biases should be addressed whenever possible to reduce error and increase the accuracy of diet estimates.

Many biases in gray wolf (*Canis lupus*) diet estimation via scat analysis have been identified (Ciucci et al. 1996, 2004, Spaulding et al. 2010), and in some cases, solutions to minimize biases have been developed (Floyd et al. 1978, Weaver and Fritts 1979, Weaver 1993). Recently, Steenweg et al. (2015) concluded that scats collected at homesites yielded a different estimated diet than scats collected on roads or trails (I refer to these as opportunistically-collected scats hereafter), which is consistent with several other studies (Theberge et al. 1978, Scott and Shackleton 1980, Fuller 1989, Trejo 2012).

However, 3 sources of potential bias—temporal (Van Ballenberghe et al. 1975, Kohira and Rexstad 1997, Tremblay et al. 2001), inter-pack (Voigt et al. 1976, Fuller 1980, Potvin et al. 1988), and age-class variability (Theberge and Cottrell 1977) —were not fully addressed prior to examining the impact of scat collection methods on diet estimates. Indeed, most studies have not accounted for all of these biases when estimating wolf diets. Thus, my objective was to 1) determine whether different scat collection methods (scats collected opportunistically, at homesites, and at GPS clusters) yield different wolf diet estimates after accounting for the 3 potential biases mentioned above, and 2) provide a practical method for estimating wolf population diet while confronting the potential biases.

Study area

My study area was in and adjacent to Voyageurs National Park (VNP; 48°30' N, 92°50' W), Minnesota, USA, an 882 km^2 protected area along the Minnesota-Ontario border. This area is in the Laurentian Mixed Forest Province, a transition zone between the southern boreal forest and northern hardwood forest (Bailey 1980). The portion of my study area south of VNP was primarily in the Kabetogama State Forest, which is actively managed for timber, resulting in a mosaic of clear cuts, young aspen (*Populus* spp.) stands, mature deciduous-coniferous stands, and wetlands. Four large lakes (Kabetogama, Rainy, Namakan and Sandpoint) cover 342 km^2 (39%) of the park and many smaller lakes are scattered throughout the landmasses in and adjacent to the park. Beaver impoundments are abundant throughout my study area, and VNP has sustained high beaver densities for over 40 yr (Johnston and Windels 2015). Lakes freeze during late

October to mid-November with ice-out occurring during late April to early May (Kallemeyn et al. 2003).

White-tailed deer (*Odocoileus virginianus*) are common in this area while moose (*Alces americanus*) are relatively rare (Windels and Olson 2016). Wolf densities are high (4–6 wolves/100 km^2) in the park with average home ranges of 115.8 km^2 (VNP unpubl. data). Coyotes are rare in the study area. Hunting and trapping are not allowed in the park. However, harvesting of white-tailed deer (*Odocoileus virginianus*), American beaver (*Castor canadensis*), and other furbearers is legal south of the park. Wolves were federally protected throughout Minnesota during my study but wolves were occasionally illegally killed outside VNP (VNP, unpubl. data).

Materials and methods

Wolf capture and collaring

Wolves from 4 packs (Ash River Pack, Moose River Pack, Sheep Ranch Pack, Shoepack Lake Pack) were captured during 2012–2015 using #7 EZ Grip foothold traps (Livestock Protection Company, Alpine, Texas). Wolves were immobilized with 10 mg/kg ketamine and 2 mg/kg xylazine using a syringe pole. Once immobilized, wolves were fitted with global positioning system (GPS) telemetry collars (Lotek IridiumTrackM 1D or 2D, Lotek Wireless Inc, Newmarket, Ontario, Canada; Vectronic Vertex Survey, Vectronic Aerospace, Berlin, Germany). Morphological measurements, tissue samples, and blood were collected. Sex and age also were recorded. Wolves were reversed with 0.15 mg/kg of yohimbine, and monitored through recovery. Fix intervals of GPS collars were set to 20 minutes, 4 hours, 6 hours or 12 hours, depending on the collar type, where the pack was located, and whether or not there was >1 collar in the pack at that time. All capture and handling of wolves was approved by the National Park Service's Institutional Animal Care and Use Committee (protocol MWR_VOYA_WINDELS_WOLF). I estimated home ranges during the ice-free season (April–October) using the 95% adaptive kernel home range method and the Home Range Tools 2.0 extension for ArcGIS (Mills et al. 2006).

Scat collection

I collected wolf scats from 4 packs from April 2015 to October 2015. I collected scats opportunistically (roads and trails), at homesites, and at GPS clusters when possible. Clusters were defined as consecutive locations that were within 200 m of each other for ≥4 hours (Latham 2009). I identified wolf homesites using location data from GPS-collared wolves or from triangulation via howl surveys. I collected scats at homesites after wolves had left the homesite or at the end of each month. I differentiated between adult and pup scats at homesites, assuming that scats with a diameter <2.5 cm were pup scats, and those >2.5 cm were adult scats (Ausband et al. 2010, Stenglein et al. 2010). I omitted scats with a 2.5 cm diameter. I assumed that scats collected opportunistically or at GPS clusters were only from adult wolves. I collected scats opportunistically in known wolf home ranges on the same network of trails and roads every 1 to 3 weeks as well as at the end of each month to ensure a known month of deposition.

I sterilized the scats by transferring them to nylon stockings and placing them in boiling water for >45 min (Chenaux-Ibrahim 2015). I then washed the scats in a washing machine, and allowed them to air dry for >12 h. I identified prey remains in each scat using the point-frame method (Ciucci et al. 2004). Briefly, this method entails placing a grid with 12 randomly-selected points over the spread-out dried scat contents and selecting 12 hairs (1 from each of 12 randomly-selected points), which are identified to species and age class, where possible, based on their micro- and macroscopic characteristics (Chenaux-Ibrahim 2015). When necessary, I made casts of the cuticula using all-purpose household cement. After all hairs were identified, each scat was visually examined to verify all prey items had been identified. If >1 prey item was present in a scat, I estimated the volume of each prey item to the nearest 5% (Tremblay et al. 2001; Chavez and Gese 2005). I considered trace amounts of hair detected (i.e., ≤10 individual hairs) from 1 prey item as 1% of the scat.

I used Weaver's (1993) regression equation (Eq. 1) to estimate percent biomass from percent volume.

$$\hat{Y} = 0.439 + 0.008 \times X \qquad \text{Eq. 1}$$

In Equation 1, X is the live mass of a prey species and Ŷ is the prey mass per scat. The percent biomass is calculated by multiplying the prey mass per scat by the percent volume.

I used a live mass of 4 kg for deer fawns from May and June, 14 kg for July and August, and 75 kg for an adult deer from June to August (Fuller 1989, Chenaux-Ibrahim 2015). I was only able to differentiate between adult and neonate ungulate hair until the end of August. As a result, I estimated the live mass of deer consumed by wolves from September and October using the ratio of 7 adults:3 fawns found at kill sites in and around the study area in the fall to give weighted mean masses of 60.9 kg in September and 63.3 kg in October (Fuller 1989). I considered an adult moose to be 444 kg and a calf to be 20 kg from May to June (Chenaux-Ibrahim 2015). I only documented adult moose in wolf diet during May–August and calves during May–June. I used 14.4 kg and 16.7 kg for the spring (April–June) and fall (July–October) live mass of a beaver, respectively, based on beaver trapping data (Windels, unpubl. data) and the average age of wolf-killed beavers in the area (Gable, unpubl. data). I used 1.5 kg for snowshoe hares (*Lepus americanus*), 0.25 kg for small mammals, and 100 kg for black bears (*Ursus americanus*) (Chenaux-Ibrahim 2015). I converted percent volume of berries (primarily *Vaccinum* spp. and *Rubus* spp.) to biomass using a conversion factor of 0.468 kg/scat (Gable, unpubl. data).

I determined how many scats/pack/month should be collected to estimate monthly pack diets using rarefaction curves (Prugh et al. 2008, Dellinger et al. 2011). To do so, I randomly subsampled without replacement from the scats collected from each pack each month, and determined diet diversity (Shannon's diversity index) as each scat was added to the monthly sample (Prugh et al. 2008). I repeated this 100 times and took the mean of the 100 simulations to yield a rarefaction curve. I used 9 categories (adult deer, fawn deer, adult moose, calf moose, beaver, berries, black bear, small mammals, snowshoe hare) to assess diet diversity.

I used 5 categories (adult deer, fawn deer, adult moose, beaver, other) for comparison of diet estimates between packs, months, scat collection methods, and age classes (Steenweg et al. 2015). Scats in the other category consisted of snowshoe hare, berries, black bear, small mammals, and in 2 instances, calf moose. To determine the diet during a particular sampling period >1 month (*e.g.*, denning season), I averaged the monthly diet estimates to yield an estimate for the larger period. I considered the denning season to be 5 months (April–August), and the ice-free season to be 7 months (April–October).

I use the term population to denote any time 2 or more pack diet estimates were combined. I did this to determine if, and how biases would change when several pack diets were combined into a single diet estimate. I estimated the diet of the population as the mean of the estimated pack diets of interest. To minimize any temporal bias when comparing diet estimates, I omitted monthly diet estimates from the denning or ice-free season diet estimates if a sufficient number of scats could not be collected from both packs, methods, or age-classes during that month (*e.g.,* I omitted May when comparing differences in collection methods from Sheep Ranch).

The comparisons used to test for the potential biases in diet estimates can be found in Table 2.1. I did not compare adult and pup scats from the Sheep Ranch Pack because I only collected 9 pup scats over the course of the denning season. Similarly, I did not examine differences in sampling method from the Shoepack Lake Pack because I was not able to collect a sufficient sample over several months from the 3 sampling methods to accurately compare whether there were differences in sampling methods.

I determined whether diet estimates differed using Fisher's Exact Tests (Trites and Joy 2005). I used an $\alpha = 0.05$ for statistical tests. When >1 statistical test was used to test a single hypothesis, I used the Bonferroni correction (α/number of statistical tests) to reduce the probability of making a type 1 error. For example, I used an α of 0.025 (0.05/2) to determine whether adult and pup diet were different because I ran 2 statistical tests (1 for the Moose River and Ash River Packs) to test the hypothesis.

I used a percentile bootstrap approach to determine the 95% confidence intervals of diet estimates by using 1 000 bootstrap simulations and then selecting the 25th and

975th highest values for each food item in a particular diet estimate (Andheria et al. 2007). All analyses were completed using program R (version 3.1.3, R Core Team 2015).

Results

I collected 2 406 scats (1 985 adult scats, 511 pup scats) from April 2015 to October 2015 (Table 2.2). Most rarefaction curves (96%; $n = 28$) appeared to reach an asymptote once 10–20 scats were included in the sample (Fig. 2.1), which suggests a sample size of 10–20 scats/month/pack was adequate to estimate diet at the scales I used.

I found no differences (Fig. 2.2) during the denning season between diet estimates derived from scats collected opportunistically and scats collected at homesites for the Ash River Pack ($p = 0.752$, $\alpha = 0.05/4$), Moose River Pack ($p = 0.400$; $\alpha = 0.05/4$), Sheep Ranch Pack ($p = 0.536$; $\alpha = 0.05/4$), or the population ($p =0.820$, $\alpha = 0.05/4$). I found no differences (Fig. 2.2) during the denning season between diet estimates derived from scats collected at homesites and scats collected at clusters for the Ash River Pack ($p =0.625$; $\alpha = 0.05/3$), Moose River Pack ($p = 0.031$; $\alpha = 0.05/3$), and the population ($p = 0.224$, $\alpha = 0.05/3$). I found no differences (Fig. 2.2) during the denning season between diet estimates derived from scats collected at homesites and scats collected at clusters for the Ash River Pack ($p = 0.441$; $\alpha=0.05/3$), Moose River Pack ($p = 0.065$, $\alpha=0.05/3$), and the population ($p = 0.363$, $\alpha = 0.05/3$). I found no difference (Fig. 2.3) during the ice-free season between diet estimates derived from scats collected opportunistically and scats collected at clusters for the Ash River Pack ($p = 0.273$; $\alpha = 0.05/3$), Moose River Pack ($p = 0.114$; $\alpha = 0.05/3$), and the population ($p = 0.540$; $\alpha = 0.05/3$).

Adult and pup diets of the Ash River Pack were different ($p < 0.025$; $\alpha = 0.05/2$) but adult and pup diets of the Moose River Pack were not ($p=0.273$; $\alpha=0.05/2$; Fig. 2.4).

Although I only collected 10 Ash River pup scats during May, the rarefaction curve appeared to reach an asymptote at 10 scats, which suggested my sample size was adequate.

Because sampling method did not impact diet estimates, I pooled scats collected via different sampling methods for each pack, and estimated pack diet from April to October for each of the 4 packs. There was a difference ($p<0.0083$; $\alpha=0.05/6$; Fig. 2.5A) in diet between every pack except the Moose River and Shoepack Lake Pack ($p=0.0097$). Population diet estimates differed between consecutive months ($p<0.0083$; $\alpha=0.05/6$; Fig. 2.5B) except between September and October ($p=0.029$).

Discussion

Scat collection methods

I determined that scat collection method had no impact on wolf diet estimation at the pack or population level after I accounted for temporal, inter-pack, and age-class variability. My study is unique in that I obtained a robust sample of scats that allowed me to test assumptions related to each of these factors concurrently. Theberge et al. (1978), Scott and Shackleton (1980), Fuller (1989), Marquard-Peterson (1998), Trejo (2012), and Steenweg et al. (2015) concluded that scats collected at homesites yielded different diet estimates than those collected opportunistically (e.g., roads, trails, etc.). However, none of these authors accounted for temporal, inter-pack, and/or age-class variability, which makes their conclusions regarding sampling method inconclusive, especially their conclusions concerning the mechanism that results in the supposed differences in diet estimates (*see* Theberge et al. 1978, Steenweg et al. 2015). In addition to not addressing all 3 of these biases, Theberge et al. (1978), Marquard-Peterson (1998), and Steenweg et al. (2015) used frequency of occurrence of food items to estimate wolf diets instead of percent biomasss–which is the most accurate method available to estimate carnivore diets from scats (Klare et al. 2011)–which could have led these researchers to conclude that scat collection method impacts diet estimates.

Although I did not find a difference between diet estimates based on scats collected at clusters and those collected via other methods (opportunistically or at homesites), this result should be interpreted cautiously because I was not able to collect a sufficient number of scats (10–20 scats/pack/month) from GPS clusters to conclude that diet estimates from GPS clusters were the same as those from other methods. Collecting scats at GPS clusters is problematic as the quantity and content of the scats collected can depend on how a cluster is defined (length of interval and how close locations must be), and how many clusters are actually visited. Clusters that span a longer timeframe could be biased toward kill sites of larger ungulate prey, thus biasing overall diet estimation (Webb et al. 2008). As the variation between prey sizes in wolf diet increases (e.g., from snowshoe hare to adult moose), this bias would increase. Similarly, scats at clusters during the ice-free season are more likely to be from the same individual instead of the entire pack because pack cohesion is weakest during this time (Demma et al. 2007, Barber-Meyer and Mech 2015). Thus, individual characteristics such as the age or breeding status of the collared wolf could bias diet estimates. Moreover, scats collected at kill site clusters could represent the same prey meal and be highly auto-correlated in space and time, which could potentially bias diet estimates (Marucco et al. 2008). Thus, I recommend that researchers not base wolf diet estimates solely on scats collected at GPS clusters.

Inter-pack variability

I documented several potential biases other than scat collection method that could have impacted diet estimates were they not accounted for. Most notably, there was inter-pack variability among every pack except the Shoepack and Moose River packs (Fig. 2.5A). Inter-pack variability in diet probably results from the differing abundance of available prey in each territory (Fuller and Keith 1980), or packs specializing on a particular prey item. Thus, it seems likely that there is less variability between individuals within a pack than between packs. Therefore, I suggest that packs should be the sample unit when estimating the diet of a population. With packs as the sample unit, scats from different packs should not be pooled. Rather, the diet of each pack should be estimated, and then the pack diets averaged to yield the diet of the population of interest. Pooling scats from several packs, which is common in wolf diet studies (Van Ballenberghe et al. 1975, Theberge et al. 1978, Fritts and Mech 1981, Fuller 1989, Forbes and Theberge 1996, Latham et al. 2011, Steenweg et al. 2015, Chenaux-Ibrahim 2015), should be avoided unless each pack is adequately and uniformly sampled. Otherwise, the packs that are most easily sampled will be over-represented.

Age-class variability

Most wolf scat studies have pooled adult and pup scats collected at homesites with the assumption that pup and adult diet is the same (Van Ballenberghe et al. 1975, Theberge et al. 1978, Fritts and Mech 1981, Steenweg et al. 2015). In my study, this assumption was valid for the Moose River Pack, but not for the Ash River Pack. Differences between adult and pup diet estimates suggests certain pack members (e.g. breeding males and females) bring disproportionally greater amounts of food to the pups than other members, or that pups are consuming food items that are abundant around homesites (Van Ballenberghe et al. 1975, Theberge and Cottrell 1977, Fuller 1989). There was no difference in pup and adult diets at homesites in Grand Teton National Park (Trejo 2012) whereas pup scats in Kluane National Park contained more small mammals than adult scats due to a colony of ground squirrels near the homesite (Theberge and Cottrell 1977). Further research is needed to determine the factors that affect differences in pup and adult diet (e.g., prey densities, prey base composition, pack composition, geography).

The best way to reduce bias associated with age class is to differentiate between pup and adult scats collected at homesites using an appropriate size cutoff while acknowledging such cutoffs are imperfect. Many studies have considered scats <25 mm in diameter to be pup scats (Latham 2009, Ausband et al. 2010, Stenglein et al. 2010, 2011) although others have used more conservative estimates of <15–20 mm (Theberge and Cottrell 1977, Trejo 2012, Derbridge et al. 2012) I used <25 mm as the cutoff to differentiate between adult and pup scats at homesites. However, I acknowledge that some adult wolf scats were almost certainly classified as pup scats using this cutoff (*see* Weaver and Fritts 1979) as 25 mm is an arbitrary and untested cutoff. Nonetheless, I believe there was little misclassification of pup scats as adult scats because pups were substantially smaller than adults (Van Ballenberghe and Mech 1975) during this period (May–August).

As pups approach adult size, bias from age class variability cannot be minimized (unless genetic techniques are used) as adult and pup scats will be indistinguishable. When pup diet is different from adult diet, pooling scats could bias overall summer wolf diet estimation. The impact of this bias would increase as the proportion of pup scats relative to adult scats at homesites increases. Thus, I suggest providing pup diet estimates alongside adult diet estimates as adult diet is a better metric for summer wolf pack diet as pups are incapable of hunting large prey.

Temporal variation

Wolf diet changes quickly in response to the availability and abundance of vulnerable prey (Van Ballenberghe et al. 1975, Fuller 1989, Theberge and Theberge 2004, Wiebe et al. 2009). Indeed, wolf diet in my study differed between consecutive months except September and October (Fig. 2.5B). Despite this, scats from several months are commonly pooled together with the implicit assumption that wolf diet is similar in every month of the larger sampling period (*e.g.,* season or year). My results indicate that such pooling introduces potentially significant bias into diet estimates. For example, beavers composed a substantial proportion (0.42) of wolf diet in the VNP area during April–May, and fawns composed a substantial proportion (0.40) during June–August. If I had collected more scats during April–May than June–August and pooled all scats I would have overestimated beaver in wolf diet during this period. The extent to which particular prey items would be over or underestimated would only increase as the disparity in sample size among months increases. In theory, scats could be pooled for a season as long as there is equal sampling in each month. However, equal scat sampling rarely occurs in scat-based diet studies.

Thus, I recommend estimating monthly diet in order to minimize potential bias from temporal variability in diet estimates regardless of the sample size collected in each month. I acknowledge that a monthly sampling period is somewhat arbitrary but it provides a convenient period that should capture intra-seasonal variability in wolf diet while still being logistically feasible. Further, this period is widely used in diet studies and should allow for broader comparisons within and among different study areas.

Determining an adequate sample size

Given the temporal and inter-pack variability in wolf diets, adequate numbers of scats from each pack each month are needed to correctly estimate the diet of the larger population. I suggest researchers collect ≥10–20 scats/pack/month to estimate monthly wolf diets (2.. 1). Because wolf diet diversity has little impact on the sample size needed (Dellinger et al. 2011, Chenaux-Ibrahim 2015, Fig. 2.1), it is not surprising that multiple studies have determined that 10–30 scats were sufficient to estimate wolf diets regardless of the time interval (monthly, seasonal, annual) over which scats were collected, or whether scats were collected from individual packs or populations. For example, 20 scats were deemed sufficient to estimate the annual diet of red wolf (*C. rufus*) packs (Dellinger et al. 2011) and 15–30 scats appeared sufficient to estimate the seasonal diet of wolf populations in Minnesota (Chenaux-Ibrahim 2015). However, rarefaction curves can determine how many scats would be needed to adequately represent the pool of scats collected but they cannot confront or account for the biases that could be present in the pool of scats collected (Trites and Joy 2005). Therefore, diet estimates can be inaccurate even when adequate sample sizes have been collected. Many researchers simply pool scats from months, seasons or years to increase sample sizes, but doing so introduces a new source of bias in an attempt to remove another.

Collecting ≥10–20 scats/pack/month could be challenging for researchers studying the food habits of remote wolf packs/populations. Although 10-20 scats would be ideal, 5-10 scats/month may be more practical in such areas and will likely still provide reasonably accurate (Fig. 2.1) monthly pack diet estimates. Regardless of sample size, researchers should calculate measures of precision around their diet estimates by using bootstrapping or other statistical approaches.

Setting a higher standard for scat-based wolf diet studies

I have demonstrated that temporal, inter-pack, and age-class variability can bias scat-based wolf diet estimates, yet most wolf diet studies have not confronted these biases. Therefore, a higher standard is necessary. To accurately estimate wolf diets, I recommend future studies strive to account for 1) monthly variability in diet, 2) inter-pack variability in diet, 3) age class variability in diet, and 4) differences in wolf diet estimates due to scat collection methods. Based on my results, I suggest all 4 of these potential biases can be minimized by collecting ≥10–20 adult scats/pack/month from homesites and/or opportunistically. Addressing the potential biases I have identified can be done in a practical and reasonable manner, but is contingent on a well-developed study design that identifies the packs that are both representative of the larger population, and that can be realistically sampled (Trites and Joy 2005, Steenweg et al. 2015). Failure to follow these recommendations could lead to incorrect conclusions about wolf diets because diet estimates could contain substantial bias. However, I am confident that using this approach will increase the quality and accuracy of wolf diet estimates, which could ultimately influence management decisions.

References

Andheria, A. P., Karanth, K.U., and Kumar, N.S. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. J. Zool. **273**(2): 169–

175. doi:10.1111/j.1469-7998.2007.00310.x.

Ausband, D.E., Mitchell, M.S., Doherty, K., Zager, P., Mack, C.M., and Holyan, J. 2010. Surveying predicted rendezvous sites to monitor gray wolf populations. J. Wildl. Manage. **74**(5): 1043–1049. doi:10.2193/2009-303.

Bailey, R. G. 1980. Description of the ecoregions of the United States. U. S. Department of Agriculture, Miscellaneous Publication No. 1391, 77 p.

Barber-Meyer, S., and Mech, L.D. 2015. Gray wolf (*Canis lupus*) dyad monthly association rates by demographic group. Can. Wildl. Bio. & Manage. **4**(2):163–168. Available from http://cwbm.name/wp-content/uploads/2016/04/7-Vol-4-Issue-2-Barber-Meyer-and-Mech.pdf [accessed 22 July 2016].

Chavez, A. S., and Gese E.M. 2005. Food habits of wolves in relation to livestock depredations in Northwestern Minnesota. Am. Mid. Nat., **154**(1):253–263. doi: 10.1674/0003-0031(2005)154[0253:FHOWIR]2.0.CO;2.

Chenaux-Ibrahim, Y. 2015. Seasonal diet composition of gray wolves (*Canis lupus*) in northeastern Minnesota determined by scat analysis. M.Sc. thesis, Department of Biology, University of Minnesota-Duluth, Duluth, MN.

Ciucci, P., Boitani, L., Pelliccioni, E.R., Roco, M., and Guy, I. 1996. A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. Wildl. Bio. **12**(1). doi:10.5297/ser.1201.002.

Ciucci, P., Tosoni, E., and Boitani, L. 2004. Assessment of the point-frame method to quantify wolf *Canis lupus* diet by scat analysis. Wildl. Bio. **10**(2): 149–153. Available from https://www.researchgate.net/publication/242145735_ Assessment_of_the_point-frame_method_to_quantify_wolf_Canis_lupus_diet_ by_scat_analysis [accessed 22 July 2016].

Dellinger, J.A., Ortman, B.L., Steury, T.D., Bohling, J., and Waits, L.P. 2011. Food habits of red wolves during pup-rearing season. Southeast. Nat. **10**(4): 731–740. doi:10.1656/058.010.0412.

Demma, D. J., Barber-Meyer, S., and Mech, L.D. 2007. Testing Global Positioning System Telemetry to Study Wolf Predation on Deer Fawns. J. Wildl. Manage. **71**(8): 2767–2775. doi: 10.2193/2006-382.

Derbridge, J.J., Krausman, P.R., and Darimont, C.T. 2012. Using Bayesian stable isotope mixing models to estimate wolf diet in a multi-prey ecosystem. J. Wildl. Manage. **76**(6): 1277–1289. doi:10.1002/jwmg.359.

Floyd, T.J., Mech, L.D., and Jordan, P.A. 1978. Relating wolf scat content to prey consumed. J.of Wildl. Manage. **42**(3): 528–532. doi:10.2307/3800814.

Forbes, G.J., and Theberge, J.B. 1996. Response by wolves to prey variation in central Ontario. Can. J. of Zool. **74**(8): 1511–1520. doi:10.1139/z96-165.

Fritts, S.H., and Mech, L.D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildl. Monogr. **80**: 3–79. doi:10.2307/3830611.

Fuller, T.K. 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. **105**: 3–41. Available from http://www.jstor.org/stable/3830614 [accessed 22 July 2016].

Fuller, T.K., and Keith, L.B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. **44**(3): 583–602. doi:10.2307/3808006.

Kallemeyn, L.W., Holmberg, K.L., Perry, J.A., and Odde, B.Y. 2003. Aquatic synthesis for Voyageurs National Park. U.S. Geological Survey, Information and Technology Report 2003-0001.

Klare, U., Kamler, J.F., and MacDonald, D.W. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. Mamm. Rev. **41**(4): 294–312. doi:10.1111/j.1365-2907.2011.00183.x.

Kohira, M., and Rexstad, E.A. 1997. Diets of wolves, *Canis lupus*, in logged and unlogged forests of southeastern Alaska. Can. Field Nat.**111**(3): 429–435. Available from http://biodiversitylibrary.org/page/35599330 [accessed 22 July 2016].

Latham, A.D.M. 2009. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta. Ph.D. dissertation. Department of Biological Sciences. University of Alberta, Edmonton, AB.

Latham, A.D.M., Latham, M.C., Mccutchen, N.A., and Boutin, S. 2011. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. J. Wildl. Manage. **75**(1): 204–212. doi:10.1002/jwmg.28.

Marquard-Petersen, U. 1998. Food habits of arctic wolves in Greenland. J. Mamm. **79**(1): 236–244. doi:10.2307/1382859.

Marucco, F., Pletscher, D.H., and Boitani, L. 2008. Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. J. Mamm. **89**(3): 665–673. doi:10.1644/07-mamm-a-005r3.1.

Mills, K. J., Patterson, B.R., and Murray, D.L. 2006. Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. Wildl. Soc. Bull. **34**(5): 1463–1469. doi:10.2193/0091-7648(2006)34[1463:EOVSFO]2.0.CO;2.

Potvin, F., Jolicoeur, H., and Huot, J. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. Can. J. Zool. **66**(6): 1274–1279. doi:10.1139/z88-186.

Prugh, L.R., Arthur, S.M., and Ritland, C.E. 2008. Use of faecal genotyping to determine individual diet. Wildl. Bio. **14**(3): 318–330. doi:10.2981/0909-6396.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Scott, B.M., and Shackleton, D.M. 1980. Food habits of two Vancouver Island wolf packs: a preliminary study. Can. J. Zool. **58**(6): 1203–1207. doi: 10.1139/z80-166

Spaulding, R., Krausman, P.R., and Ballard, W.B. 2010. Observer bias and analysis of gray wolf diets from scats. Wildl. Soc. Bull. **28**(4): 947–950. doi:10.2193/2009-305.

Steenweg, R., Gillingham, M.P., Parker, K.L., and Heard, D.C. 2015. Considering sampling approaches when determining carnivore diets: the importance of where, how, and when scats are collected. Mamm. Res. **60**(3) 1–10.doi:10.1007/s13364-015-0222-4.

Stenglein, J.L., Waits, L.P., Ausband, D.E., Mack, C.M., and Zager, P. 2010. Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. J. Wildl. Manage. **74**(5): 1050–1058. doi:10.2193/2009-305.

Stenglein, J.L., Waits, L.P., Ausband, D.E., Zager, P., and Mack, C.M. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. J. Mamm. **92**(4): 784–795. doi:10.1644/10-MAMM-A-200.1.

Theberge, J.B., and Cottrell, T.J. 1977. Food habits of wolves in Kluane National Park. Arctic. **30**(3): 189–191. doi: 10.14430/arctic2699.

Theberge, J.B. and Theberge, M.T. 2004. The wolves of Algonquin Park, a 12 Year Ecological Study. Department of Geography, Publication Series Number 56, University of Waterloo, Waterloo, Ontario.

Theberge, J.B., Oosenbrug, S.M., and Pimlott, D.H. 1978. Site and seasonal-variations in food of wolves, Algonquin Park, Ontario. Can. Field. Nat. **92**(1): 91–94. Available from http://biodiversitylibrary.org/page/28062334 [accessed 22 July 2016].

Trejo, B.S. 2012. Comparison of two methods used to characterize the summer diet of gray wolves (*Canis lupus*). M.Sc. thesis, College of Natural Resources and Sciences, Humboldt State University, Arctata, CA.

Tremblay, J.P., Jolicoeur, H., and Lemieux, R. 2001. Summer food habits of gray wolves in the boreal forest of the Lac Jacques-Cartier Highlands, Québec. Alces **37**(1):1–12. Available from https://www.researchgate.net/publication/236736451_Summer_food_habits_of _gray_wolves_in_the_boreal_forest_of_the_Lac_Jacques-Cartier_highlands_Quebec [accessed 22 July 2016].

Trites, A.W., and Joy, R. 2005. Dietary analysis from fecal samples: how many scats are enough? J. Mamm. **86**(4): 704–712. doi:10.1644/1545.

Van Ballenberghe, V., and Mech, L.D. 1975. Weights, growth, and survival of timber wolf pups in Minnesota. J. Mamm. **56**(1): 44–63. doi:10.2307/1379605

Van Ballenberghe, V., Erickson, A.W., and Byman, D. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildl. Monogr. **43**: 3–43. Available from http://www.jstor.org/stable/3830388 [accessed 22 July 2016].

Voigt, D.R., Kolenosky, G.B., and Pimlott, D.H. 1976. Changes in summer foods of wolves in central Ontario. J. Wildl. Manage. **40**(4): 663–668. doi:10.2307/3800561

Wachter, B., Blanc, A., Melzheimer, J., Höner, O.P., Jago, M., and Hofer, H. 2012. An advanced method to assess the diet of free-ranging large carnivores based on scats. PLoS ONE 7:e38066. doi:10.1371/journal.pone.0038066.

Weaver, J.L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. J. Wildl. Manage. **57**(3): 534–538. doi:10.2307/3809278

Weaver, J.L., and Fritts, S.H. 1979. Comparison of coyote and wolf scat diameters. J. Wildl. Manage. **43**(3): 786–788. doi:10.2307/3808765.

Webb, N.F., Hebblewhite, M., and Merrill, E.H. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. J. Wildl. Manage. **72**(3): 798–807. doi:10.2193/2006-566.

Wiebe, N., Samelius, G., Alisauskas, R.T., Bantle, J.L., Bergman, C., de Carle, R., Hendrickson, C.J., Lusignan, A., Phipps, K.J., and Pitt, J. 2009. Foraging behaviours and diets of wolves in the Queen Maud Gulf Bird Sanctuary, Nunavut, Canada. Arctic. **62**(4): 399–404. doi:10.14430/arctic171.

Windels, S. K., and Olson B.T. 2016. Moose population survey at Voyageurs National Park: 2016. Natural Resource Data Series NPS/VOYA/NRDS—2016/1031. National Park Service, Fort Collins, Colorado.

Table 2.1. Statistical comparisons used to identify the biases in wolf (*Canis lupus*) diet estimates from 4 wolf packs in and adjacent to Voyageurs National Park, MN during April–October 2015.

Potential Bias	Comparisons[a]	Time Period[b]	Packs Used[c]	No. of Tests[d]	α [e]	p < α?
Scat collection method						
	Opp vs. Home	Denning	AR,MR,SR,POP	4	0.013	No
	Opp vs. Clusters	Denning	AR,MR,POP	3	0.017	No
	Home vs. Clusters	Denning	AR,MR,POP	3	0.017	No
	Opp vs. Clusters	Ice-Free	AR,MR,POP	3	0.017	No
Inter-pack variability						
	AR vs. MR	Ice-Free	AR,MR	6	0.008	Yes
	AR vs. SR	Ice-Free	AR,SR	6	0.008	Yes
	AR vs. SHOE	Ice-Free	AR,SHOE	6	0.008	Yes
	MR vs. SHOE	Ice-Free	MR,SHOE	6	0.008	No
	MR vs. SR	Ice-Free	MR,SR	6	0.008	Yes
	SR vs. SHOE	Ice-Free	SR,SHOE	6	0.008	Yes
Temporal variability[f]						
	Apr vs. May		POP	6	0.008	Yes
	May vs. Jun		POP	6	0.008	Yes
	Jun vs. Jul		POP	6	0.008	Yes
	Jul vs. Aug		POP	6	0.008	Yes
	Aug vs. Sep		POP	6	0.008	Yes
	Sep vs. Oct		POP	6	0.008	
Age-class variability						
	AR adult vs. pup	May-Aug	AR	2	0.025	Yes
	MR adult vs. pup	May-Aug	MR	2	0.025	No

[a]Opp = opportunistic, Home = homesites.
[b]Denning season = Apr–Aug, Ice-free season = Apr–Oct.
[c]AR = Ash River pack, MR = Moose River pack, SR = Sheep Ranch pack, SHOE = Shoepack Lake pack, and POP denotes anytime ≥2 pack diet estimates were combined.
[d]Number of Fisher's Exact Tests used to test a particular hypothesis.
[e] Critical Value determined via Bonferroni Correction (α = 0.05/no. of statistical tests).
[f]All 4 pack diets averaged to yield diet of population.

Table 2.2. Number of adult wolf (*Canis lupus*) and pup scats from 3 different collection methods (GPS-clusters, homesites, and opportunistic) from 4 wolf packs in and adjacent to Voyageurs National Park, MN during April–October 2015.

			Month							
Pack	Age	Method	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Total
Ash River	Adult	Clusters	23	6	3	4	-	4	19	59
		Home	16	34	19	55	28	-	-	152
		Opp.	21	19	15	17	11	16	17	116
		Total	60	59	37	76	39	20	36	327
	Pup	Home	-	10	27	57	28	-	-	122
Moose River	Adult	Clusters	8	16	8	36	3	39	42	152
		Home	99	36	75	121	34	-	-	365
		Opp.	10	16	31	38	36	10	6	147
		Total	117	68	114	195	73	49	48	664
	Pup	Home	-	26	201	118	44	-	-	389
Sheep Ranch	Adult	Clusters	-	1	-	-	-	-	19	20
		Home	11	-	21	30	17	-	-	79
		Opp.	23	47	83	43	84	47	10	337
		Total	34	48	104	73	101	47	29	436
Shoepack[a]	Adult	Total	51	54	29	32	108	60	134	468
Total			**262**	**265**	**512**	**551**	**393**	**176**	**247**	**2406**

[a]Scats pooled from opportunistic collections (April–July) and from homesites and clusters (Sept–Oct).

Fig 1.1. Examples of evidence found at beaver kill sites (A,B,C), and of wolf behavior when in active beaver habitats (D) in Voyageurs National Park 2015. A) Matted vegetation at kill sites provided important information about how wolves killed beavers. B) Wildlife technician A. Homkes stands at Beaver Kill Site 13 < 10 m below an active beaver dam. C) Beaver Kill Site 18 on a small point < 5 m from the active dam where a wolf, based on the trampled vegetation, presumably pulled a kit beaver out of the water and consumed it. D) A wolf bed (lower left corner) found when examining clusters of GPS-locations in the spring. The wolf bedded for ≥ 8 hr next to this active beaver lodge without making a kill.

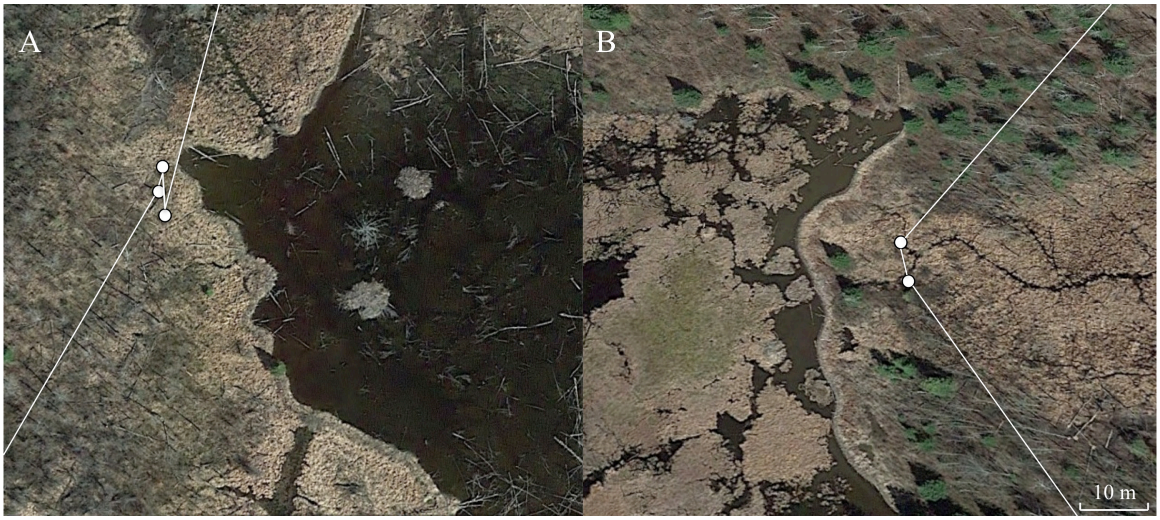

Fig 1.2. Locations (solid circles) and line from previous location from a GPS-collared wolf (4–hr fix interval) in Voyageurs National Park during April–May 2015 when A) at Beaver Kill Site 2 and B) when bedded next to a small channel below an active beaver dam (Map data: Google, DigitalGlobe).

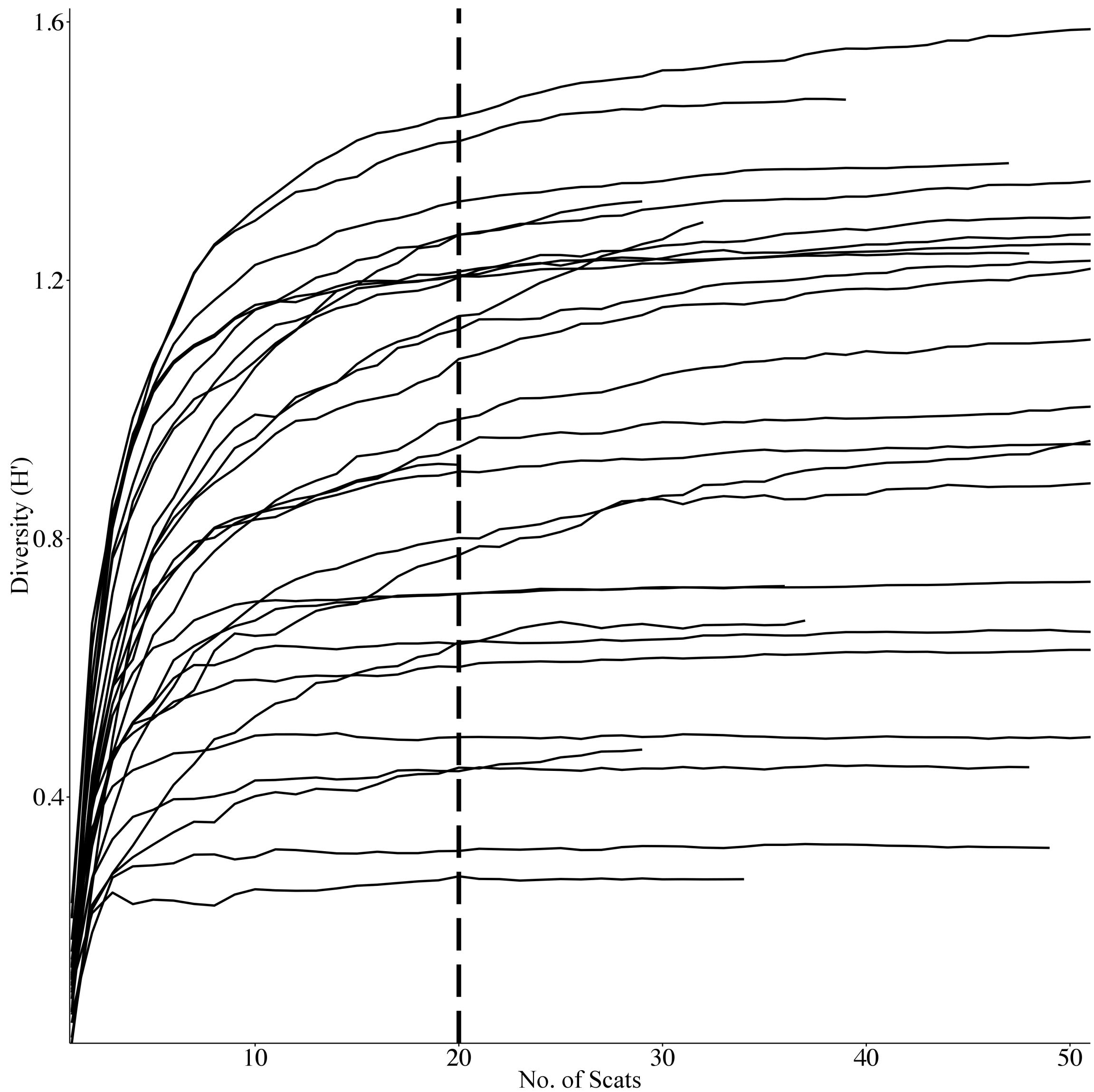

Fig. 2.1. Rarefactions curves examining the impact of scat sample size on 2015 monthly (April–October) wolf (*Canis lupus*) pack diet diversity in Voyageurs National Park, Minnesota. The dotted vertical line represents when most curves have reached an asymptote.

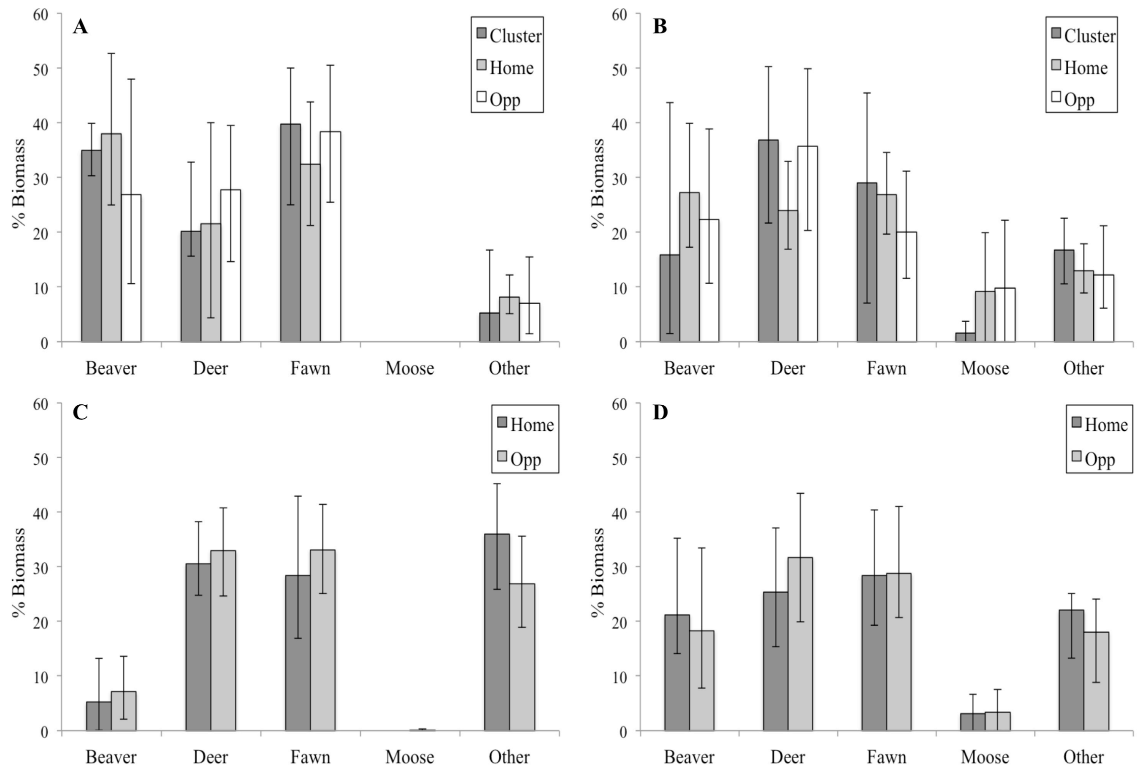

Fig. 2.2. Estimated diet of 3 wolf (*Canis lupus*) packs–Ash River Pack (A), Moose River Pack (B), Sheep Ranch Pack (C)–and the population (D) in and adjacent to Voyageurs National Park based on 3 scat collection methods (clusters, homesites, and opportunistic) during the 2015 denning season (April–August). Error bars represent the 95% confidence intervals.

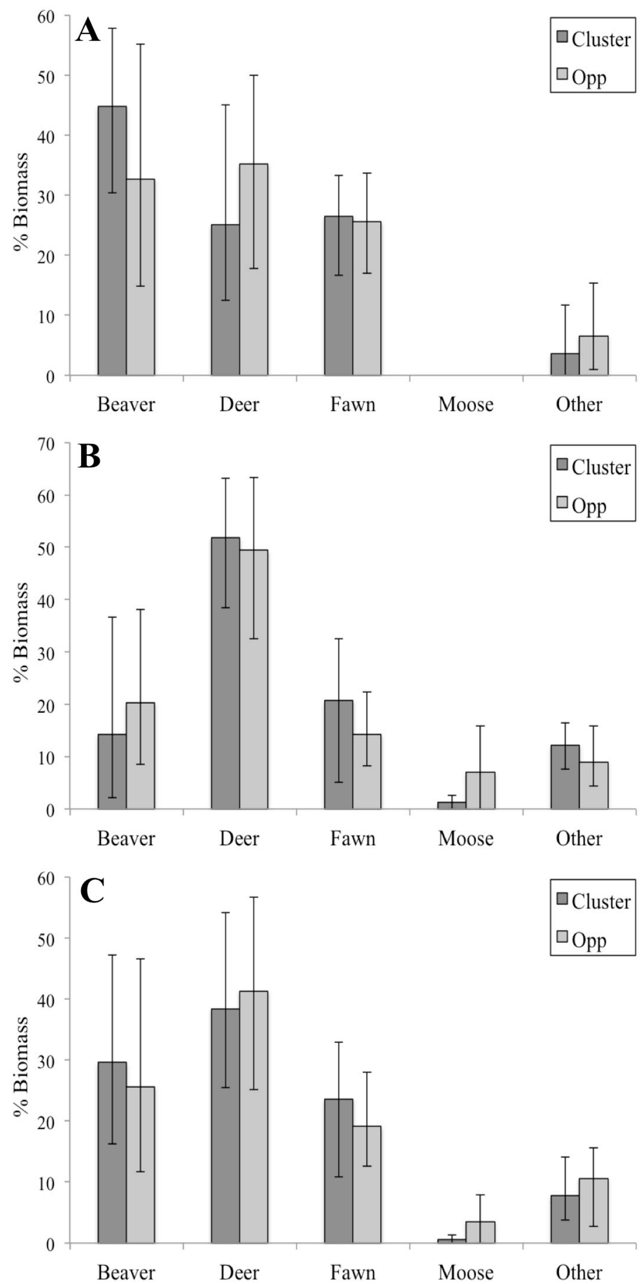

Fig. 2.3. Estimated diet of 2 wolf (*Canis lupus*) packs–Ash River Pack (A), Moose River Pack (B)–and the population (C) in and adjacent to Voyageurs National Park based on 2 scat collection methods (at clusters and opportunistically) during the 2015 ice-free season (April–October). Error bars represent the 95% confidence intervals.

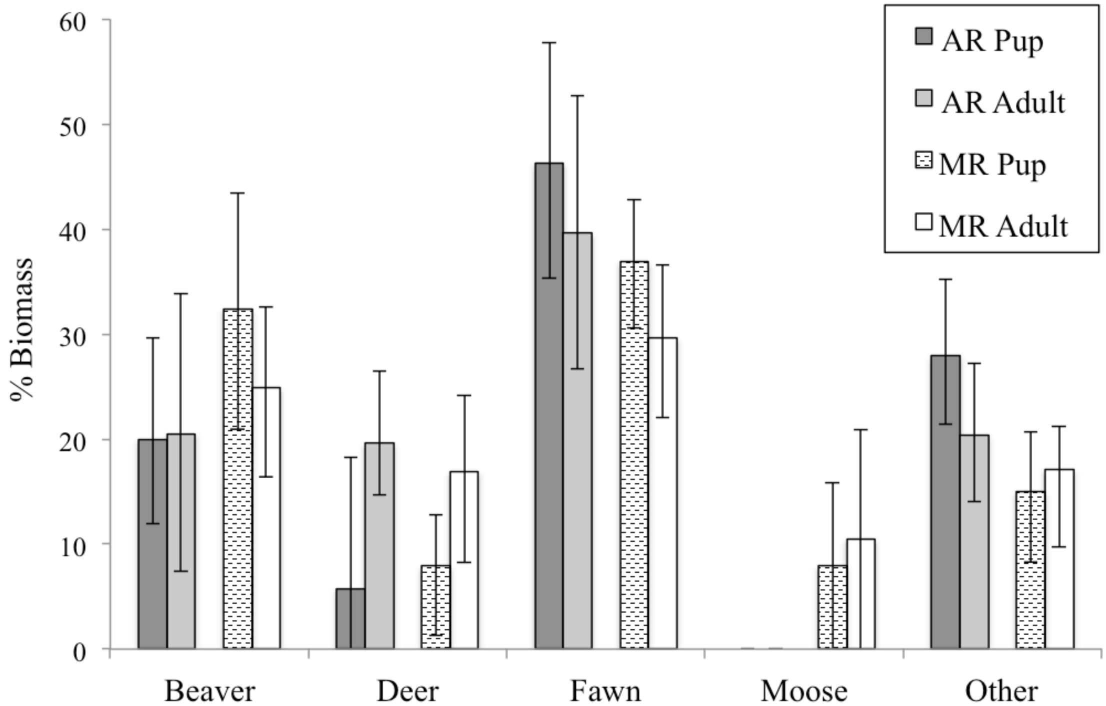

Fig. 2.4. Comparison between adult and pup wolf (*Canis lupus*) diet for the Ash River and Moose River packs from May–August 2015. Error bars represent the 95% confidence intervals.

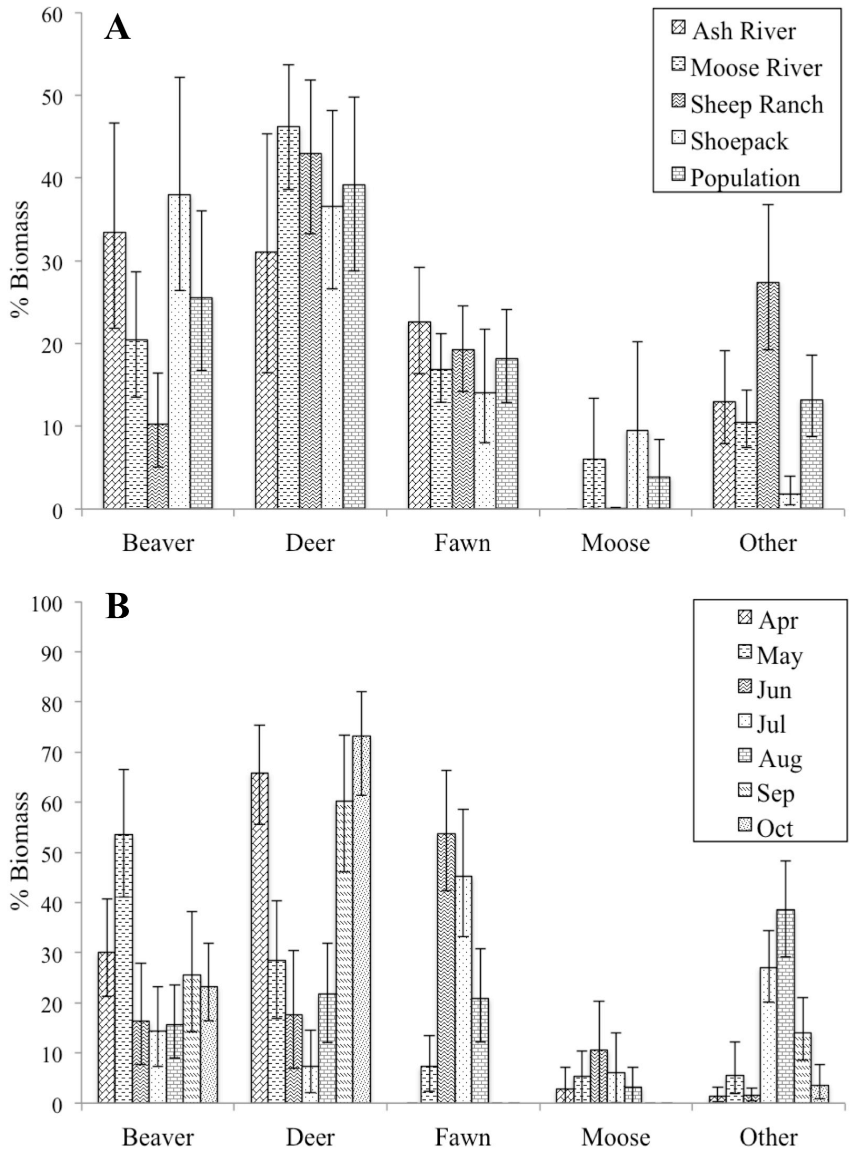

Fig. 2.5. Inter-pack (A) and monthly (B) variability in wolf (*Canis lupus*) diet in and adjacent to Voyageurs National Park from April 2015–October 2015. Error bars represent the 95% confidence intervals.

APPENDIX A

DESCRIPTION OF INDIVIDUAL BEAVER KILL SITES

Below are descriptions of 22 beaver kill sites that I documented from April 2015 to November 2015 in Voyageurs National Park, Minnesota. When describing a kill site I frequently mention the location of beaver remains, or of the collared wolf as being in the vicinity of the kill site. I considered an object in the vicinity of the kill site if it was <200 m from the kill site but not at the kill site. I use the term consumption site to denote the location where a wolf consumed the beaver. In most cases the consumption occurred at the kill site. However, there were a few instances where multiple wolves were present and several consumption sites radiated out from the actual kill site (e.g., Beaver Kill Site #17 and 22). With many of the individual descriptions I have attempted to infer how the beaver was killed based on evidence at the kill site, and wolf behavior at other clusters I examined in similar locations where I did not find kill sites. In some instances there simply was not enough evidence to determine how the wolf or wolves killed the beaver, and any attempts to describe how the beaver was killed are purely speculative.

Descriptions of Individual Kill Sites

Beaver Kill Site #1 (UTM 501767, 5361064)

Kill Site Type: Below Dam

On 27 April 2015 I documented a beaver kill site from wolf V009 of the Ash River Pack. The wolf spent a minimum of 20 hr (4-hr fix interval) in a grassy area downstream from a beaver dam during which at some point it killed a beaver. There were many beaver trails going over the dam and 1 went into a small stagnant channel (approximately 1–1.5 m wide) below the dam that connected to an old beaver pond. I found 4 wolf beds in this cluster within 3 m of each other. Given the amount of time spent at this cluster, I am unsure if these 4 beds are from a single wolf or multiple wolves. The beds were 15–20 m from the dam. In 2 of the wolf beds I found tufts of beaver hair and bone fragments. Beaver hair, dried stomach contents, and beaver bones in a small trampled area about 10 m from the beds suggested this was where the beaver was killed and consumed. This site was 15.0 m downstream from the dam. Trampled vegetation next to the stagnant channel suggested the wolf pulled the beaver out the channel and then consumed it 10 m away.

Beaver Kill Site #2 (UTM 505335, 5361076)

Kill Site Type: Below Dam

On 28 April 2015 I documented a beaver kill site from wolf V009 of the Ash River Pack. The kill occurred below a large beaver dam. There were well-worn trails and fresh cuttings on the downstream side of the dam suggesting that beavers used this area frequently. Although the kill site was close to a well-worn feeding trail that crossed over the dam, I considered this to be a below dam kill site because it was <10 m from a large dam. At the kill site I found a large area of depressed vegetation with small tufts of beaver fur, a few dried pieces of stomach contents, and a few bone fragments. The wolf appeared to have been alone and spent a minimum of 8 hr (4-hr fix interval) at this kill site. I postulate that the beaver crossed over the dam unaware of a wolf waiting below the dam, and once on the downslope of the dam was attacked immediately.

Beaver Kill Site #3 (UTM 505477, 5363871)

Kill Site Type: Near Shore

On 30 April 2015, I documented a kill site from wolf V009 of the Ash River Pack 27.2 m from the shoreline at the south end of Mud Bay, Lake Kabetogama. The kill site was easily identified as there were large amounts of beaver fur present as well as a large area of matted vegetation. A wolf scat was also present at the kill site. The wolf was probably alone at this kill and stayed there a minimum of 12 hr (4-hr fix interval).

The kill site was in a large open grassy area with the nearest woody vegetation approximately 50 m further inland. There were no beaver trails nearby and there was no evidence of fresh cuttings in the vicinity. The beaver was likely associated with an active lodge that was about 100 m away. I am uncertain how the beaver got from the water to the kill site.

Beaver Kill Site #4 (UTM 505642, 5363788)

Kill Site Type: Near Shore

I documented Beaver Kill Site #4 on 30 April 2015 100 m from Beaver Kill Site #3. This kill site was found opportunistically and based on GPS-location data wolf V009 was not near this site on the date this kill occurred. Thus, the kill was made by another wolf in the Ash River pack. Beaver Kill Site #4 was undoubtedly a different kill site as it was 1–2 days old (based on the fresh wolf scat as well a the bright red, fresh tissue on skull fragments) while Beaver Kill Site #3 was 17 days old (based on GPS-location data).

Without a GPS-collared wolf at the kill site I cannot determine how long the wolf was present at the kill site but it appears to have been alone. The only remains at the kill site were skull fragments including the incisors, a piece of the lower mandible, and the upper molariform teeth. There was depressed vegetation at the site but as was the case with Beaver Kill Site #3, I am uncertain what occurred here. The kill site was 16 m from a small channel at the end of the bay that had < 0.3 m of water in it. There were no fresh cuttings or beaver trails nearby, and I am not sure why the beaver was at this area.

Beaver Kill Site #5 (UTM 504262, 5363766)

Kill Site Type: At Lodge

On 30 April 2015 I documented a kill site approximately 10 m from a beaver lodge on the west side of Daly Bay in Lake Kabetogama, VNP. The lodge was situated on a 10 m wide channel in tall cattails (*Typha* spp.) and canary grass (*Phalaris arundinacea*). The water level was very low and the entire lodge was out of the water. The channel was mostly dry with some water (about 1.0 m wide by 0.5 m deep) remaining. To access open water, beavers would have to travel 50–70 m via the channel.

Numerous wolf tracks surrounded the lodge. There were also wolf tracks in the muddy canal entrances to the lodge where a wolf was presumably inspecting the lodge. Wolf V009 of the Ash River pack appeared to be alone and spent a minimum of 8 hr (4-hr fix interval) at this kill site. Based on depressed vegetation, it appeared wolf V009 made contact with the beaver 1 m from the lodge and then dragged it back behind the lodge 10 m where it then consumed the beaver. This kill site was especially obvious because the dead cattails and canary grass were very brittle and broke easily with contact.

The intact beaver skull, tufts of fur, and bone fragments were at the kill site. I think the wolf waited for the beaver to exit the lodge and then attacked it. I saw no evidence in the muddy shoreline that the beaver tried to run back into the lodge with the wolf in pursuit. Therefore, the beaver had to have been leaving the lodge when attacked.

Beaver Kill Site #6 (UTM 523575, 5359361)

Kill Site Type: Near Shore

On 3 May 2015, I documented a kill site on the west shore of Little Johnson River about 1 km north of Little Johnson Lake. The kill was 16.0 m from water and wolf V028 of the Moose River pack spent a minimum of 6 hr (6-hr fix interval) in the vicinity of the kill. The wolf was likely by itself at the kill.

Like other on shore kill sites, I do not know what occurred here. The kill site was in an open grassy area next to the river with no beaver trails or active cuttings nearby. I found the skull, lower mandible, bone fragments and fur at the kill site. This beaver was likely associated with an active lodge ~150 m away. The colony had dammed the Little Johnson River about 50 m upstream of the kill site. There were no drag marks or depressed vegetation nearby.

Beaver Kill Site #7 (UTM 518406, 5360343)

Kill Site Type: Feeding Trail

On 5 May 2015, I documented a kill site on the south shore of Moose River approximately 1.5 km upstream from where Moose River flows into Moose Bay, Namakan Lake. Wolf V027 spent a minimum of 12 hr (6-hr fix interval) in the vicinity of this kill site, and was probably alone.

The kill site was on a feeding trail by an active beaver lodge situated on Moose River where beavers were cutting small aspen saplings. The kill occurred 17.7 m from

Moose River. At the kill site I only found beaver fur and stomach contents. I did find tufts of beaver fur up to 1 m high in the vegetation from when the wolf was handling the beaver at the kill site.

Wolf tracks on exposed muddy shoreline of Moose River provided helpful information in understanding what occurred at this kill. I located a wolf bed close to an active beaver lodge on Moose River as well as tracks on the shoreline from the lodge to the feeding trail (distance from lodge to feeding trail was about 30 m) where the wolf tracks stopped and turned up the trail. I found tufts of beaver hair every few meters along the feeding trail until I reached the kill site. I concluded the wolf was waiting nearby when a beaver left the lodge and went ashore on this feeding trail. The wolf followed, cut off the beaver's access to water, and killed it. The tufts of fur along the trail are probably from the wolf dragging or chasing the struggling beaver up the trail.

Beaver Kill Site #8 (UTM 504617, 5360090)

Kill Site Type: Feeding Trail

On 8 May 2015 I documented a kill site from wolf V009 of the Ash River pack on the west side of the west fork of Daley Bay. Wolf V009 had spent a minimum of 9.0 hr at the kill site (the collar recorded locations at a 4 and then 5 hr fix interval). The kill site was 98.9 m from water and in a dense coniferous stand with a few deciduous trees scattered throughout. Close by were many feeding trails leading inland and the beavers appeared to be actively cutting >50 m from water in several places. The kill site was inconspicuous as it was in a coniferous stand and thus disturbances from the kill were not easily identified. However, after searching extensively I found the kill site. The only remains were long bones with some flesh still attached. I found a few fresh wolf scats and some more bone fragments in the vicinity. Based on the number of scats and scattered remains as well as several sets of wolf tracks on the shoreline, I do not think wolf V009 was alone at this kill site.

Determining what occurred at this kill site was challenging, and it is puzzling how far from water this kill occurred. With so many feeding trails nearby, it seems likely that the beaver was foraging far from water when either the beaver detected wolves, or was attacked by wolves. However, there were no fresh cuttings within 40 m of the kill site. With multiple wolves present, the beaver likely had no way to reach the water. Perhaps the beaver tried to escape by running the opposite direction of the wolves which would explain why the kill occurred even farther inland than the farthest freshly cut tree. I did not find any evidence of drag marks that would suggest the beaver was dragged to the kill site. Moreover, I thoroughly searched the entire area and ruled out the possibility that the beaver was killed closer to water and then consumed where I found the remains.

Beaver Kill Site #9 (UTM 507859, 5364552)

Kill Site Type: Below Dam

On 12 May 2015, I documented a kill site near a group of 3 ponds about 1.5 km west of Blind Ash Bay, Lake Kabetogama. Wolf V009 of the Ash River Pack was here for a minimum of 6 hr. Unlike at all the other kill sites, I found no remains at this kill. Between when the kill would have occurred and when I was able to examine the cluster there was heavy rain which certainly could have washed tufts of fur or little pieces of stomach contents to the bottom of the depressed vegetation. Similarly, it is not unreasonable that the wolves consumed the entire carcass. For example, at a few kill sites

I have not found any hair and at others only hair. Therefore it is likely that either all the remains were consumed, or the few that were not were washed away and not found.

However, several other lines of evidence suggest this was in fact a kill site. I found 3 viscous, tar-like scats indicative of a recent kill (Peterson and Ciucci 2003) that all contained beaver hair. Moreover, at the GPS-locations I found a large area that had been trampled and all the vegetation depressed. This area was significantly larger than a wolf bed and was of the same size and shape as that of Beaver Kill Sites #2 and #13. I have examined >150 clusters and have not documented depressed vegetation such as this except at other beaver kill sites.

The location of this kill fits the pattern seen at other below dam kill sites. The matted vegetation suggests the beaver was in the small channel below the dam when it was attacked and then consumed nearby on shore. Wolf V009 appeared to have been with at least 1 other wolf at this kill site based on the number of beds present. Over the course of the summer, wolf V009 visited this area frequently and I determined that in July 2015 wolf V009 killed a deer fawn and a great blue heron (*Ardea herodias*) chick <50 m from the location of this kill site. Similarly, wolf V009 killed a beaver (Beaver Kill Site #14) at the same pond as this kill site in October.

Beaver Kill Site #10 (UTM 508927, 5361953)

Kill Site Type: Small Waterway

On 15 May 2015, I documented a kill site in the middle of the Ash River territory near a small creek that was flowing into an active beaver pond. Wolf V009 appeared to be alone when attacking and killing this beaver. Based on drag marks from the creek to the kill site, it appears that wolf V009 attacked the beaver in the water and then consumed it 8.2 m away. Moreover, there was a fresh wolf track in the mud of the creek right where it appeared the beaver was attacked. The track was pointed the direction I would have expected if the wolf attacked the beaver and tried to drag it out of the creek by backing up. The creek was narrow and shallow with most of the creek <0.5 m deep.

I found a few tufts of beaver fur at the kill site and on vegetation between the kill site and the creek presumably from when the wolf was dragging the beaver to the kill site. Nearby I found a wolf scat. Wolf V009 was at the kill site for a minimum of 4 hr (4-hr fix interval). As I searched the area I identified a rudimentary dam about 25 m upstream from the kill site. Close by were several freshly cut aspens that were likely being used to construct a dam and thus stop the flow of the creek. This dam was approximately 250 m upstream from an active beaver pond that the creek flowed into. I concluded that the beaver was likely a dispersing beaver that was trying to dam up the stream and create a pond when it was killed.

Beaver Kill Site #11 (UTM 521515, 5359451)

Kill Site Type: Small Waterway

On 2 June 2015, I documented a kill from wolf V027 from the Moose River Pack. The kill occurred about 150 m south of Wiyapka Lake next to a small waterway that went through an alder swamp. The small waterway flowed into Wiyapka Lake from a beaver pond complex 300–400 m upstream. The kill site was easily identified by the trampled vegetation, presence of stomach contents, and a large amount of beaver hair. There was a foul odor from the remains (this is the only kill site where that was the case).

I do not know how long wolf V027 was in the area because there was only 1 location taken within 200 m of the kill site. However, the maximum time spent at the kill site was 8 hr (4-hr fix interval). Technically, this kill site did not occur at a cluster as there were no other locations prior to, or after this location within 200 m. I only visited this location because it was between 2 clusters I had to investigate. The kill site was within 5 m of the GPS location. It is worth noting that the wolf spent at least 12 hr only 225-250 m west of the kill site prior to being located at the kill site.

Based on the depressed vegetation and proximity of the kill to water, it appeared the wolf attacked the beaver in the small waterway and then consumed it 1 m away on land. There were no fresh cuttings or beaver trails nearby to suggest the beaver was on land when caught. The small channel that the beaver was pulled from was about 2–3 m wide and >1 m deep.

Beaver Kill Site #12 (UTM 515479, 5346542)

Kill Site Type: Forest Interior

On 6 June 2015, I documented a kill from V026 of the Sheep Ranch Pack. Wolf V026 was present at the kill site for at least 12 hr (12-hr fix interval). The kill site was approximately 1 km southwest of Corner Lake in a dense aspen stand 222.1 m away from the nearest body of water. I did not find any evidence of fresh cuttings or any other beaver activity. Therefore, I presumed this was a dispersing beaver that was trying to move from 1 pond complex to the next by crossing through the forest. Wolf V026 had ventured 1 km south of the Sheep Ranch Pack territory on the same day and likely encountered the beaver opportunistically.

At the kill site I found evidence of a struggle as a downed log had been torn apart on 1 end with claw and/or tooth marks present in the wood. A small sapling had also been broken off about 1 m above the ground, and I found beaver fur on the sapling where it had been broken off. More beaver fur was found in the vegetation nearby, and at the kill site. I also found a wolf scat at the kill site. About 15 m away from the kill site I found some bone fragments that were in the same spot as the second GPS location from wolf V026. It appeared that wolf V026 was alone at the kill site as all beaver remains that were identified were found at the GPS locations from that wolf.

Beaver Kill Site #13 (UTM 511374, 5363576)

Kill Site Type: Below Dam

On 10 October 2015, I documented a kill site 75 m west of the Sullivan Bay trailhead below a dam near an active pond. The kill occurred below the 2nd active dam downstream of the pond instead of the primary dam that was damming the main pond. The 2 dams were about 30 m apart, and a well-used beaver trail crossed over the primary dam, across a small stretch of land and into the small pond created by the 2nd dam. There was also a trail that crossed over the 2nd dam to a small shallow channel below the dam. The kill site was about 3 m from the trail and 10 m below the second dam (distance to the small channel was 4 m). I speculate that the beaver had crossed over the second dam and had almost reached the small channel when a wolf, concealed in the vegetation, attacked the beaver and consumed it close by.

The kill site was obvious due to the large area of trampled vegetation but I found very little of the carcass at this location (a tuft of beaver fur and stomach contents). Wolf V009 of the Ash River pack was present in the vicinity of the kill site for at least 24 hr (6-hr fix interval). However, between 6 and 12 hr the wolf moved 140 m away where he bedded down for at least another 18 hr on a high rocky ridge. I found 3 fresh wolf scats on this ridge – all were associated with GPS-locations. Similarly, I found the beaver skull close by 1 of the GPS-locations. Based on this V009 was likely alone at the kill site.

Beaver Kill Site #14 (UTM 507558, 5364569)

Kill Site Type: Feeding Trail

On 13 October 2015, I opportunistically documented a kill site on the southwest side of the beaver pond where Beaver Kill Site #9 was found. AlthoughI found this kill site opportunistically, I think that wolf V009 killed this beaver because GPS-collar data (6-hr fix interval) shows that he was 170 m from the kill site about 2 hr after I found it. I do not think it is coincidence that the wolf was within the vicinity of this kill site just after I documented a freshly-killed beaver.

The kill occurred on an active feeding trail where beavers had been cutting and transporting aspen to the pond. Wet blood across the ground and vegetation suggested the kill site was < 12 hr old. Rain throughout the previous day would have washed away the blood if the kill had occurred before or during this time.

At the kill site I found intact segments of the intestinal tract and fresh pieces of muscle tissue that had not been consumed. I probably scared the wolf away from the carcass as I did not find these remains at any other kill site. I also found a piece of leg bone still attached in the socket to a piece of the pelvis. Some tufts of beaver fur were spread around the kill site and stomach contents had been strewn about. The wolf appeared to be alone as all beaver remains found were at the kill site. I searched the area extensively and did not find any beaver remains or beds in the vicinity of the kill. I do not know how long Wolf V009 remained or would have remained at the kill site had I not scared it away.

On the shore of the pond I found a set of fresh wolf tracks in the mud. The tracks were on the west side of the feeding trail and headed east along the pond shore. I did not find any tracks in the stretches of exposed muddy shoreline on the east side of the feeding trail leading me to believe the wolf stopped traveling on the shore when it reached the feeding trail. This seems likely and is consistent with how wolf V027 hunted and killed a beaver on a feeding trail at Beaver Kill Site #7. I do not know whether this wolf was waiting until the beaver went on shore, or was running the shoreline when it caught the fresh scent of a beaver, turned onto the feeding trail, and found the beaver inland. Whatever the case, the beaver appeared to be cutting a recently-felled aspen when, based on the drag marks and blood on the vegetation, it was attacked and then consumed about 10 m away. The kill site was 15.5 m from the pond.

Beaver Kill Site #15 (UTM 505693, 5360680)

Kill Site Type: Feeding Canal

On 13 October 2015, I documented a kill site on the south shore of the east fork of Daley Bay, Lake Kabetogama. Wolf V009 of the Ash River Pack was present at this kill site for at least 6 hr (6-hr fix interval) and appeared to be alone. The dead beaver was from the same lodge as the beaver found at Beaver Kill Site #16.

This kill site was 4.9 m from an active feeding canal that was about 30–35 m long, 1 m wide, and about 1 m deep. Depressed vegetation from the shore of the canal to the consumption site suggests the wolf attacked the beaver in the water and then consumed it away from the canal. I only found a few small tufts of beaver fur, stomach contents, a few bone fragments, and 2 castor glands. I did not find any fresh cuttings or other beaver activity at the kill site. Thus, there is no reason to believe the beaver was on shore when attacked. The beaver was likely pulled out of the water about half way down the feeding canal. There was no evidence (depressed vegetation or tracks) on the shoreline to suggest the wolf attempted to pull the beaver out of the canal at any other spot.

Thus, I think the beaver was heading toward the feeding trail at the end of the feeding canal and wolf V009 was waiting in the tall grass on the canal edge. Wolf V009 then attacked and killed the beaver. The depressed and trampled grass at the kill site made it easy to identify. However, very little of the beaver was left.

Beaver Kill Site #16 (UTM 505770, 5360683)

Kill Site Type: Feeding Canal

On 13 October 2015, I documented a kill site on the north shore of the east fork of Daley Bay. The kill occurred near Beaver Kill Site #15 and the beaver killed at this kill site (#16) belonged to the same lodge as the beaver at Beaver Kill Site #15. Wolf V009 of the Ash River pack spent at least 30 hr (6-hr fix interval) at this kill site. I believe multiple wolves were present because I found several scats, and consumption sites within 50 m of the kill site.

The beaver appeared to have been pulled out of a wide feeding canal, dragged on shore, and consumed 2.6 m from water. The canal was not a narrow, long canal like at Beaver Kill Site #15 but rather was short and funnel shaped as the mouth of the canal was quite wide but then narrowed to about 1 m when it met the shore. Given the shape of the canal and angle of the shoreline, the canal was likely >1 m in most places.

The beaver was attacked 3 m from the end of the canal. Wolf V009 or another wolf it was with were likely waiting on the canal edge and attacked the beaver as it was heading for the feeding trail at the end of the canal. The beavers had been especially active at this feeding trail and had likely cut more than half of the trees that were <30 m from shore.

I left this kill site at dusk and howled to elicit a wolf response. Within seconds the entire Ash River Pack (4 adults, 2 pups) howled back to the northeast of the kill site. The 2 pups in the pack could be heard clearly, and I estimated that the wolves were no farther 300 m away.

Wolf V009 first arrived in the vicinity of the kill site on 11 October 2015 and the last location at the kill site was on 12 October 2015 at 9:30. I do not know then if it was simply coincidental that the entire pack was near this kill site at this time or if some pack members remained in the area for up to 48 hr following the kill.

Beaver Kill Site #17 (UTM 509974, 5361135)

Kill Site Type: Feeding Trail

On 26 October 2015 I documented a kill site at a pond about 1 km due west of the Helipad Road. Wolf V009 of the Ash River Pack was present at this kill site for at least 12 hr (6-hr fix interval). The kill was hard to find as the few remains present were inconspicuous. I was only able to identify a few tufts of beaver fur, stomach contents and both castor glands. However, only the few small pieces of the stomach contents were present at the actual kill site.

The week preceding this kill site was generally cold, and the ground and leaf litter were frozen as a result. Thus, the evidence of a struggle or of the handling of the beaver that is usually apparent from disturbed leaf litter or vegetation was mostly missing. Nonetheless, upon searching the area I found some small pieces of stomach contents in a ‘bread crumb’ like trail back to the pond and were able to determine that the kill occurred 1 m off of a feeding trail and 5.1 m from the water. Some depressed vegetation was present at the kill site but it would not have been obvious without following the remains back to the location of the kill.

I determined that there were 2 wolves present at this kill based on the fact that I found 2 separate trails of beaver remains going in different directions from the kill site. It appeared as though 1 wolf dragged part of the beaver 20 m south –leaving a trail of stomach contents– to a consumption site. The other wolf dragged the rest of the beaver in an east-southeast direction about 25 m (leaving tufts of beaver fur caught in the vegetation) to a consumption site. I found 3 wolf scats in the vicinity of the kill. I did find a few wolf beds next to active beaver trails around this pond about 30–50 m from the kill site. However, I do not know whether the wolves waited for the beaver to come ashore or not.

Beaver Kill Site #18 (UTM 507510, 5367693)

Kill Site Type: At Dam

On 26 October 2015, I documented a kill site where wolf V045 of the Shoepack Lake Pack killed a kit beaver approximately 200–300 m north-northeast of the Shoepack Beach Campsite, Lake Kabetogama. Wolf V045 was present at this kill site for 7.7 hr (20-min fix interval). The kill occurred on a small point that jutted out into a pond about 1 m away from the beaver dam. Based on the GPS data, wolf V045 was present at the kill site on the small point for at least 1.3 hr and then moved 50 m away and bedded down for at least 6.3 hr. A scat was present at both the kill site and also where the wolf bedded down nearby. The scat at the kill site was full of beaver stomach contents but very little beaver hair. The small size of the kit might have led to the wolf consuming a significant amount of the stomach contents which were then defecated. All beaver remains found were located on the point. Wolf V045 appeared to be alone at the kill site. The only remains identified were a small pile of stomach contents and 2 small incisors indicating this was a beaver kit.

The depressed vegetation on the point suggested the beaver was in the water when wolf V045 attacked it. The beaver was then killed and consumed 1 m from the water on the point. Based on the evidence, there are 3 different ways this kill could have occurred: 1) the wolf waited on the point and a beaver swam right next to shore and the wolf grabbed it without going in the water, 2) the beaver was out in the pond a few meters from shore, the wolf waited until it was close enough and then leaped into the pond and caught it, or 3) the wolf was swimming in the water, caught the beaver, and then dragged it up onto the point.

Beaver Kill Site #19 (UTM 508825, 5350058

Kill Site Type: Feeding Trail

On 30 October 2015, I documented a kill site from the Sheep Ranch Pack at a pond approximately 1 km north of the northwest corner of the Sheep Ranch. Wolf V026 was present at the kill site but I think that the wolf was with several other wolves based on the number of beds at the kill site. The beaver pond had several long narrow channels to access feeding trails on the shore. The kill occurred on a feeding trail only 8.6 m from the water. Based on the depressed vegetation, the beaver was probably on land when attacked and killed based on the depressed vegetation.

Most of the remains present at the kill site were tufts of beaver fur on the ground. However, beaver fur was also caught in briars and other small shrubs. The lack of remains was likely due to the fact that multiple wolves were present. I found 3 wolf scats nearby. It appeared the beaver was coming from the feeding canal to the feeding trail. Once it was on shore, the wolves attacked, and consumed the beaver.

Wolf V026 was present at the kill site for at least 7.7 hr (20-min fix interval). Based on the GPS data it appeared as though the wolf spent 1–1.7 hr near the pond close to the kill. If I assume that the kill occurred when the wolf was at the exact location of the kill site then I can say that the wolf was at this beaver pond 40 min prior to making or helping make the kill. However, I do not know when the kill occurred and since there were other wolves present I do not know if wolf V026 or other pack members made the kill. Wolf V026 then moved 30 m east of the kill site and bedded down for several hr on a small ridge. Other wolf beds were present on the ridge and I think that several wolves bedded down in this area after the kill.

Beaver Kill Site #20 (UTM 515020, 5366546)

Kill Site Type: Feeding Trail

On 4 November 2015, I documented a kill site on the north shore of Kohler Bay, Lake Kabetogama. Wolf V045 of the Shoepack Lake Pack was present in the vicinity of the kill site for at least 25.7 hr (20-min fix interval). The kill site was on a feeding trail 23.1 m from the water. The beavers had been very active in this area and near the kill site there were several freshly-cut aspens.

I found this kill site easily as only 85% of the beaver had been consumed. I found the skull and lower mandible as well as the entire vertebral column with the bones of the back legs still attached. Wolf V045 was likely alone at this kill site as all beaver remains were at GPS-collar locations. Wolf V045 was initially at the kill site for at least 1.3 hr before it left for a few hours then returned and stayed for at least 24.3 hr more. The beaver was an adult based on skull size and could have weighed 18–22 kg. Therefore, it would have been a significant amount of food for a single wolf, which likely explains why the wolf was in the vicinity of the kill site for so long.

I know when this wolf arrived at the kill site but I do not know when it made the kill. All of the initial locations were <10 m apart but it is unknown whether that was the result of the wolf waiting at the kill site. I would expect the same cluster pattern from a wolf that waited and then made a kill, and from a wolf that immediately made a kill and consumed the beaver at that location.

Beaver Kill Site #21 (UTM 507733, 5364461)

Kill Site Type: Feeding Trail

On 4 November 2015, I documented a kill site at the same pond complex as Beaver Kill Site #9 and #14. Wolf V009 of the Ash River Pack was present at this kill site for at least 6 hr (6-hr fix interval). Throughout the ice-free season Wolf V009 frequently visited and spent a significant amount of time around this pond complex (V009 killed 3 beavers, 1 fawn and 1 great blue heron chick in this area).

Wolf V009 was not alone at this kill site. I found bone fragments in a few areas about 20 m from the kill site in the woods which suggests that other wolves were present. I also found several wolf beds near the kill site. One wolf scat was found approximately 30 m from the kill site.

The kill occurred on a feeding trail 12.8 m from the water. The beavers had been clearing many large aspens in the area near the kill site. I am not sure how the wolf or wolves hunted this beaver, and GPS data do not provide clarification. At the kill site I found stomach contents and tufts of beaver fur strewn across the vegetation. Some small bones and bone fragments were found at the kill site as well.

Beaver Kill Site #22 (UTM 534251, 5363143)

Kill Site Type: Feeding Trail

On 6 November 2015, I documented a kill site on the south shore of a beaver pond just north of O'Leary Lake. Wolf V033 of the Moose River Pack was present at this kill site for at least 5.3 hr (20-min fix interval). I found the kill site 13.4 m from the water on an active feeding trail. The kill was relatively fresh and I found wet blood on the leaf litter and vegetation at the kill site. The beaver appeared to have been attacked about 8 m from the pond but then dragged farther inland to where it was consumed.

I think that the entire Moose River Pack (8 adults, 3–4 pups) was present at this kill site. In the fall this pack appeared to be moving around its territory nomadically and almost every cluster I visited had several beds and scats present. Moreover, for most of the fall I had 2 GPS-collared wolves in this pack and they were almost always in the same location at the same time. I visited the clusters prior to, and after this kill and found numerous wolf beds and wolf scats at both.

At the kill site I found strewn stomach contents, a few tufts of beaver fur, and some small bone fragments. I searched the area and found several wolf beds 25-75 m from the kill site with beaver fur, beaver blood, stomach contents or bone fragments in them. Similarly I found the skull and lower mandible 180 m from the kill site in an area where a few wolves appeared to have bedded down. Whether the wolves were searching for or waiting for this beaver is unknown. Wolf V033 was at the kill site for several hr but I do not know if the wolves had made the kill yet or if they were waiting to make the kill. In the vicinity of the kill site I documented several wolf beds next to beaver feeding trails but I cannot say whether this was from wolves waiting for a beaver to come ashore, or simply the result of them bedding down after making the kill.

APPENDIX B

EVIDENCE AND DESCRIPTION OF A FAILED HUNTING ATTEMPT

On 19 June 2015, I examined a cluster of 2 locations (4-hr fix interval) from Wolf V009. The locations were 10–15 m apart and below the same active beaver dam where Beaver Kill Site #9 occurred. I found a wolf bed about 20 m below the active dam next to a small channel (1 m wide and 1-1.5 m deep) that went from the active dam to an inactive pond about 50 m east. On the edge of the channel there was a large swath of trampled grass that began 10 m below the active dam and ended at a 1 m long beaver trail used to cross over the active dam. Much of the grass had been bent over into the channel as if an animal was trying to reach an object in the channel. I found wolf hairs throughout the depressed grass. In the mud of the beaver trail that crossed over the dam, I found fresh beaver tracks and a set of fresh wolf tracks pointing towards the active pond. I found no evidence of a beaver kill common to most other confirmed sites, such as hair, blood, stomach contents, or castor glands.

Based on this evidence, I believe this was a failed beaver-hunting attempt by Wolf V009. I think that Wolf V009 was bedded below this active dam, located a beaver in the small channel, and attempted to pull it out of the channel (hence the depressed and trampled grass). I speculate that the beaver was attempting to get back to the active pond by swimming below the surface in the channel as the wolf was attempting to capture the beaver in the water. The beaver was likely able to cross over the 1-m beaver trail into the pond just before the wolf could capture it (hence the set of wolf tracks pointing towards the active pond). I documented several instances where wolves had successfully pulled beavers out of small waterways, feeding canals, and small channels below active beaver dams. Indeed, a wolf likely dragged a beaver out of the same small channel at Beaver Kill Site #9 (which occurred at the same location of this observation). Thus, this hunting strategy is effective at times. However, based on this observation, the water provides a medium through which beavers could possibly out maneuver wolves and avoid being captured.

APPENDIX C

VOYAGEURS NATIONAL PARK'S INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL

United States Department of the Interior
NATIONAL PARK SERVICE
Biological Resource Division
1201 Oakridge Drive, Suite 200
Fort Collins, Colorado 80525

National Park Service
Institutional Animal Care and Use Committee
Animal Research Protocol Approval

Principal Investigator(s): Steve Windels
Telephone: 218-283-6692
Electronic Mail: steve_windels@nps.gov
Region: MWR

Protocol Approval Number: MWR_VOYA_Windels_Wolf_2015.A3
Project Title: Investigations of Wolf Ecology in Voyageurs National Park

Approval Date: 5/21/15
Effective Date: 5/21/15

Questionnaire Dates; Years 1 and 2 (if applicable): 5/21/16, 5/21/17

Expiration/Re-Submittal Date: 5/21/18

Funding Agency(ies): NPS, University of Minnesota-Duluth

Species: *Canis lupus*- Gray Wolf

Number(s) of Animals: <20 per year

This project study was reviewed by the National Park Service Institutional Animal Care and Use Committee. The following action(s) were taken:

Project Status: Approved

Interim NPS IACUC Chair: /s/ Tim Pinion; **Date**: 5/21/15
NOTE: Immediately report any/all unexpected mortalities to the NPS IACUC as you would to your primary, approving IACUC of record.