

Weekly Summer Diet of Gray Wolves (*Canis lupus*) in Northeastern Minnesota

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ABSTRACT.—Wolves (*Canis lupus*) are opportunistic predators and will capitalize on available abundant food sources. However, wolf diet has primarily been examined at monthly, seasonal, or annual scales, which can obscure short-term responses to available food. We examined weekly wolf diet from late June to early October by collecting scats from a single wolf pack in northeastern Minnesota. During our 15 wk study, nonungulate food types constituted 58% of diet biomass. Deer (*Odocoileus virginianus*) fawns were a major food item until mid-July after which berries (primarily *Vaccinium* and *Rubus* spp.) composed 56–83% of weekly diet biomass until mid-August. After mid-August, snowshoe hares (*Lepus americanus*) and adult deer were the primary prey. Weekly diet diversity approximately doubled from June to October as wolves began using several food types in similar proportions as the summer transitioned into fall. Recreational hunting of black bears (*Ursus americanus*) contributed to weekly wolf diet in the fall as wolves consumed foods from bear bait piles and from gut piles/carcasses of successfully harvested or fatally wounded bears. To our knowledge, we are the first to examine wolf diet via scat analysis at weekly intervals, which enabled us to provide a detailed description of diet plasticity of this wolf pack, as well as the rapidity with which wolves can respond to new available food sources.

INTRODUCTION

How predators respond to changing food availability can impact predator-prey dynamics and ecosystem function (Pace *et al.*, 1999). Dietary plasticity and prey switching behavior in predators can be advantageous for capitalizing on the availability of alternate prey or persisting during periods when the primary prey species is not abundant or available. For example generalist predators, such as red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*), typically exhibit high dietary flexibility and will subsist on a variety of alternate foods when their primary prey is unavailable (Andelt and Andelt, 1984; Dell'Arte *et al.*, 2007). Conversely, more specialized predators, such as Canada lynx (*Lynx canadensis*) and cougars (*Puma concolor*), may continue depredating their primary prey during periods of reduced abundance instead of switching to alternate food sources (Villepique *et al.*, 2011; Peers *et al.*, 2012; Burstahler *et al.*, 2016).

Wolves (*Canis lupus*) are 'true carnivores' that rely primarily on ungulate prey (Peterson and Ciucci, 2003; Bosch *et al.*, 2014). However, wolves are also opportunists and will use

alternative food sources seasonally when they are abundant or vulnerable (Tremblay *et al.*, 2001; Wiebe *et al.*, 2009). For example, in coastal British Columbia and Alaska, salmon (*Oncorhynchus* spp.) can constitute up to 90% of seasonal wolf diet as wolves respond to the abundance of spawning salmon (Darimont and Reimchen, 2002; Stanek *et al.*, 2017; Watts and Newsome, 2017). Similarly, medium to large-sized rodents such as muskrats (*Ondatra zibethicus*; Chavez and Gese, 2005), woodchucks (*Marmota monax*; Messier and Crete, 1985), and beavers (*Castor* spp.; Gable *et al.*, 2016; Sidorovich *et al.*, 2017; Gable *et al.*, 2017c) can compose substantial portions of seasonal wolf diet when abundant and available.

Wolf diets have predominantly been examined via scat analysis at monthly, seasonal, and annual time scales, which can obscure short-term responses to changing food availability. The manner in which wolves respond to changing food availability provides insight into the foraging strategies and life history characteristics of wolves and can have implications for wolf-ungulate dynamics. For example, in northeastern Alberta, incidental summer adult caribou (*Rangifer tarandus*) mortality resulted from wolves selecting beaver habitats in the summer, which increased spatial overlap of wolves and caribou (Latham *et al.*, 2013).

From early to mid-summer wolves radiate out from den or rendezvous sites to forage, usually as individuals or small groups for themselves and the pups (Barber-Meyer and Mech, 2015). During this period wolves are primarily consuming small prey such as ungulate neonates, beavers, and hares (*Lepus* spp.) (Nelson and Mech, 1981; Mech *et al.*, 2015). Late summer to early fall can be an energetically taxing period for wolves, as the energetic demand of near-adult size wolf pups is high, while ungulate prey are reaching peak nutritional condition and neonates have grown to near-adult size—both of which reduce the number of vulnerable ungulate prey (Mech, 1970; Fuller *et al.*, 2003). Reduced ungulate vulnerability can force wolves to exploit other available food sources to meet energetic needs (Van Ballenberghe *et al.*, 1975). Our objective was to examine wolf diet at weekly intervals from late June to early October, to provide a detailed description of the foraging strategies of one wolf pack in a southern boreal system during the summer. We hypothesized weekly wolf diet diversity would increase during our study because wolves would have to exploit alternate food sources as vulnerable neonatal fawns transitioned to less vulnerable juveniles over summer.

STUDY AREA

Our study area was in north-central Kabetogama State Forest, Minnesota (48°33'N, 92°90'W), just south of Voyageurs National Park (Fig. 1). The Kabetogama State Forest is on the southern edge of the boreal forest and is part of the Laurentian Mixed Forest Province (Bailey, 1980). The area is actively managed for timber, which results in a mosaic of clear cuts, young aspen (*Populus tremuloides*) stands, mature deciduous-coniferous stands, and wetlands. A network of logging roads and all-terrain vehicle trails provides access throughout much of the area. White-tailed deer (*Odocoileus virginianus*), American beaver (*Castor canadensis*), and other furbearers are legally harvested in the forest. The recreational harvest of black bears (*Ursus americanus*) is a popular activity and includes use of bait piles, which were maintained as early as 2 wk before the start of the 2015 bear hunting season (1 September–18 October). Summer wolf densities in the area are 4–6 wolves/100 km² with average summer home ranges of 115.8 km² (Gable, 2016). White-tailed deer are common throughout our study area, with prefawn deer densities likely around 2–3 /km² (Gable *et al.*, 2017a). Moose (*Alces americanus*) are rare with densities likely <0.05 moose/km² (Windels, 2014). The area also sustains a dense beaver population (Johnston and Windels, 2015).

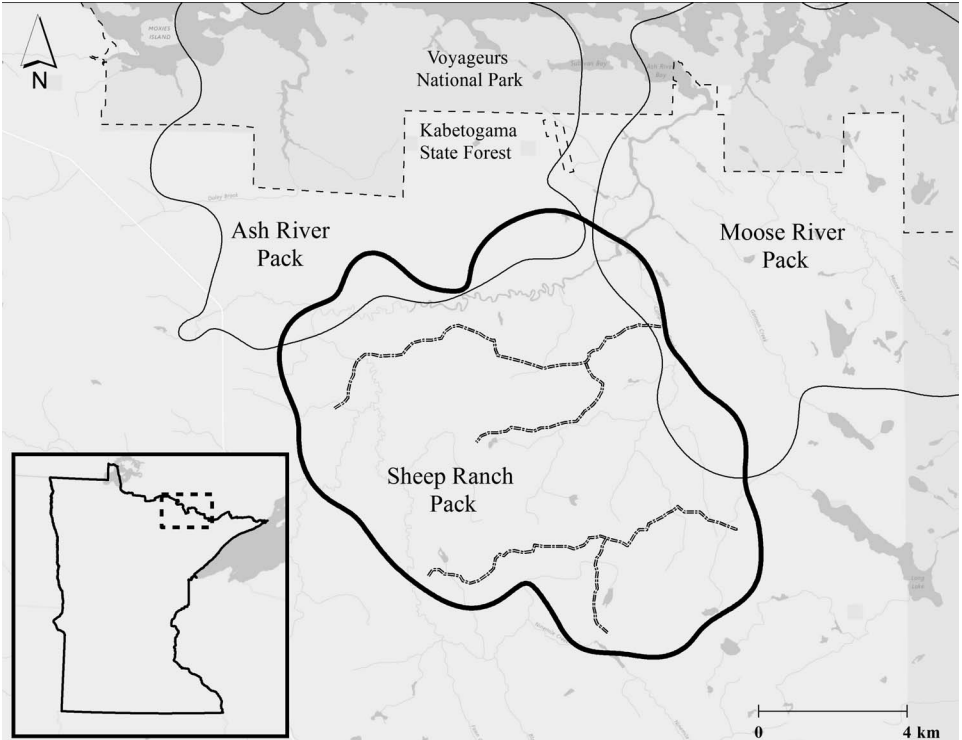


FIG. 1.—The 95% adaptive kernel home range of the Sheep Ranch wolf pack in the Kabetogama State Forest, Minnesota, Summer 2015. Scat collection routes as well as known home ranges of neighboring packs in nearby Voyageurs National Park are also shown

METHODS

WOLF CAPTURE, COLLARING, AND HOME RANGE DELINEATION

In August 2014 we captured a female wolf from the Sheep Ranch Pack using a foothold trap. The wolf was fit with a Vertex Survey GPS collar (Vectronic Aerospace, Berlin, Germany) with a 12 h fix-interval. We recaptured this wolf in August 2015 and refit it with a Lotek IridiumTrack 1D (Lotek Wireless, Inc, Newmarket, Ontario, Canada) GPS collar with a 20 min fix-interval. Wolf capture and handling procedures were approved by the National Park Service Animal Care and Use Committee (protocol approval number: MWR_VOYA_Windels_Wolf_2015A.3) and conformed to American Society of Mammalogist guidelines for care and handling of live mammals (Sikes, 2016). We estimated the Sheep Ranch Pack summer (May–October 2015) home range using the 95% adaptive kernel home range method and the Home Range Tools 2.0 extension for ArcGIS (Mills *et al.*, 2006). Minimum summer pack size was estimated based on a single track survey conducted on sandy roads in the Sheep Ranch pack territory the day after heavy rain in August 2015. We did not have pack size estimates during winter 2014–2015. The presence of pups was determined based on the presence of pup scats (<2.5 cm diameter; Stenglein *et*

al., 2010) at rendezvous sites (identified from the GPS-locations from the collared wolf) from June through August.

WEEKLY DIET DETERMINATION

We collected scats from logging roads and trails within the Sheep Ranch Pack home range from 30 June 2015 to 6 October 2015. Scats were cleared off of roads and trails on 24 June a week before the first collection, and in subsequent weeks scats were collected weekly along the same 29 km route to ensure samples were from the previous week (Fig. 1). We only collected scats >2.5 cm in diameter to avoid collecting scats from wolf pups and smaller sympatric canids (Weaver and Fritts, 1979; Stenglein *et al.*, 2010). We prepared scats for analysis, identified food types in scats, and estimated weekly diets using the methods of Gable *et al.* 2017c. In short we used the point-frame method to randomly select 12 hairs from each scat. Each of these 12 hairs were then identified to species and age class, where possible, based on their micro- and macroscopic characteristics (Chenaux-Ibrahim, 2015). We then quantified the percent volume (to the nearest 5%) of each food type in the scat via visual examination, which allowed us to estimate the percent volume of nonmammalian prey items (*e.g.*, berries) as well as the percent volume of mammalian prey remains other than hair (*e.g.*, bone, hooves, claws, etc.). We then converted percent volume diet estimates to percent biomass using Weaver's (1993) regression equation and the prey weights from Gable *et al.* (2017c; Table 1). All diet estimates are presented as percent diet biomass unless otherwise specified.

SAMPLE SIZE REQUIREMENTS AND SIMULATION

Determining how many scats must be collected to accurately estimate the weekly diet of wolves is dependent on the number of food types present and the relative proportion of each item (Prugh *et al.*, 2008). Trites and Joy (2005) suggested a minimum of 60 scats per population should be collected to document differences between populations. More recently, rarefaction curves examining the relationship between monthly wolf pack diet diversity and number of scats collected in northeastern Minnesota suggest 10–20 scats are sufficient to determine the monthly diet for a wolf pack (Gable *et al.*, 2017c). Although ≥ 10 scats/week would probably have been sufficient (Gable *et al.*, 2017c), we used a conservative sample size target of 20 scats/week for determining weekly pack diet.

If a sufficient sample size ($n \geq 20$) was collected in a given week, we used a percentile bootstrap approach to determine the 95% confidence intervals for diet estimates by using 1000 bootstrap simulations and then selecting the 25th lowest (*i.e.*, 25th/1000) and 975th (*i.e.*, 975th/1000) highest values for each food item (Andheria *et al.*, 2007). We were not able to collect ≥ 20 scats in 12 of 14 sample periods. Consequently, the pool of scats collected during a given week might not contain every prey item consumed by the pack during that week, and/or the proportion of each food item in the weekly diet might be incorrect. Therefore, to bound the uncertainty around our point estimates based on the scats collected in Week_{*t*} and determine 95% confidence intervals, we used a bootstrapping approach that allowed us to account for both of these possibilities. This involved randomly selecting 20-*n* scats (where *n* = the number of scats collected in Week_{*t*}) from a pool of scats from Week_{*t-1*}, Week_{*t*}, and Week_{*t+1*}. That is, we assumed the pool of scats from these 3 wk contained the scats we were not able to collect in Week_{*t*}. The randomly-selected scats were added to the scats collected in Week_{*t*} to estimate weekly diet and diversity. We ran this procedure 1000 times and derived 95% confidence intervals by selecting the 25th lowest and the 975th

TABLE 1.—Weekly diet of the Sheep Ranch Pack in northeastern Minnesota from late June to early October 2015 as determined by scat analysis. The percent volume of food types was estimated for each scat and then converted to percent biomass based on Weaver’s (1993) regression equation and prey weights¹ from Gable *et al.* (2017c). Shannon’s diversity index (1948) was used to estimate diet diversity

Week	Dates	n	Fawn ³		Deer ³		Berries ⁴		Hare		Beaver		Small mammal		Bear		Other ⁵		Diversity
			Vol.	Bio.	Vol.	Bio.	Vol.	Bio.	Vol.	Bio.	Vol.	Bio.	Vol.	Bio.	Vol.	Bio.	Vol.	Bio.	
Week 1	06/24–06/30	17	82	81	0	0	0	0	0	0	11	13	7	6	0	0	0	0	0.61
Week 2	07/01–07/08	21	68	72	0	0	0	0	8	7	13	14	9	8	0	0	2	0	0.89
Week 3	07/09–07/15	10	63	72	0	0	10	10	8	8	9	10	1	0	0	0	10	0	0.93
Week 4	07/16–07/23	3	35	37	3	7	62	56	0	0	0	0	0	0	0	0	0	0	0.87
Week 5	07/23–07/29	8	13	14	0	1	68	64	0	0	13	15	6	5	0	0	0	0	1.03
Week 6	07/30–08/05	17	1	1	3	7	87	83	6	5	3	4	0	0	0	0	0	0	0.67
Week 7	08/06–08/12	30	4	4	5	11	74	69	9	8	4	5	4	3	0	0	0	0	1.09
Week 8	08/13–08/19	16	16	21	4	9	68	68	0	0	0	0	2	1	0	0	10	0	0.89
Week 9	08/20–08/26	17	25	39	6	17	6	6	33	38	0	0	0	0	0	0	30	0	1.22
Week 10	08/27–09/02	10	21	21	40	66	0	0	18	13	0	0	0	0	0	0	22	0	0.87
Week 11	09/03–09/09	10	2	3	4	8	0	0	50	46	30	34	10	9	0	0	5	0	1.19
Week 12	09/10–09/16	12	8	11	18	26	0	0	46	33	23	21	2	1	3	7	0	0	1.31
Week 13	09/17–09/23	17	12	14	28	34	0	0	29	17	0	0	5	3	20	32	6	0	1.12
Week 14 ²	09/24–10/06	7	7	9	16	22	0	0	57	47	0	0	0	0	13	22	7	0	1.08
Weekly Mean:			25	27	12	15	25	24	21	18	7	8	3	3	3	3	6	7	0.99

¹ Deer fawn in June, 4 kg; deer fawn during July–August, 14 kg; adult deer during June–August, 75 kg; deer during September, 61 kg; deer during October, 63 kg; beaver, 16.7 kg; black bear, 100 kg; snowshoe hare, 1.5 kg; small mammals, 0.25 kg

² Week 14 includes Week 15 scats as well due to the small sample sizes

³ After Week 10 adult deer and fawn hair was indistinguishable. We estimated the percent volume and biomass of fawns and adults from Weeks 11–14 using the ratio seven adults: three fawns based on kill sites located in and around the study area

⁴ We converted from percent volume to percent biomass of berries using 0.468 kg/scat (Gable *et al.*, 2017)

⁵ Includes bear bait, vegetation, bird remains, and garbage; “Other” during Weeks 8–14 was almost entirely bear bait

highest percent biomass values simulated for each food item. For Week₁ we selected from a pool of scats from Weeks 1–3, and for Week₁₄ we used Weeks 12–14. We combined the scats from the last 2 wk (Weeks 14–15) into Week₁₄ because sample sizes in each week were <6.

We estimated weekly diet diversity using Shannon's Diversity Index (H' ; Shannon, 1948; Prugh *et al.*, 2008). We used simple linear regression to test whether diet diversity and the number of food types consumed per week increased over time. We used $\alpha = 0.05$ for our hypothesis tests. Simulations and statistical analyses were conducted using the program R (R Core Team; 2015).

RESULTS

We collected a total of 195 scats from the Sheep Ranch Pack with a mean of 13 scats/week (range: 3–30 scats; Table 1). We collected ≥ 10 scats in 78% (11/14) of the weeks during our study. The Sheep Ranch Pack had a minimum of six adult wolves during the collection period. We determined the Sheep Ranch Pack had ≥ 1 pup based on the presence of pup-sized scats (<2.5 cm; Stenglein *et al.*, 2010) at rendezvous sites searched during our collection period. Summer home range (95% kernel) was estimated as 101 km² (Fig. 1) with minimal overlap with two adjacent packs to the north.

Deer fawns (27%) and berries (24%) were the primary food types for the Sheep Ranch Pack during our study (Table 1). Snowshoe hare and adult deer made up 18% and 15% of pack diet, respectively, with beaver, black bears, and small mammals composing the remaining 16%. We did not detect any moose.

WEEKLY DIET

Deer fawns were the primary food item (72–81%) during 24 June–15 July (Fig. 2A). The percent biomass of deer fawn in the diet declined precipitously after 15 July, and during 30 July–12 August composed only 3% of pack diet. The percent of deer fawn in the diet then increased from mid-August to early September, composing 27% of weekly diet during 13 August–2 September (Fig. 2A). After 2 September deer fawns only constituted 10% (range: 3–14%) of weekly diet. Adult deer composed 4% of the diet from 24 June–19 August. However, at the end of August and into the rest of the fall, adult deer composed a substantial part of weekly diet, constituting 28% (range: 8–66%) of pack diet during 20 August–6 October.

As deer fawn decreased in diet, berries (primarily *Vaccinium* spp. and *Rubus* spp.) became the primary food type and composed 68% (range: 56–83%) of weekly diet during 16 July–19 August (Figs. 2C–F). Berries were only detected during 9 July–26 August. Snowshoe hare made up a small percentage of the diet during 24 June–19 August but were a substantial food item during 20 August–6 October, constituting 34% (range: 13–47%) of weekly wolf diet, making it the primary food item during this period. Beavers were a small percentage ($\leq 13\%$) of the diet except during 3 September–16 September (28% of the weekly diet). Small mammals constituted 3% of wolf diet (Fig. 2F).

Black bear remains (*i.e.*, meat, hide, bones) composed 26% of diet biomass during 17 September–6 October. Bear baits dispensed for bear hunting (primarily almonds, peanuts, pumpkin and sunflower seeds, and candies) became common in wolf scats during 13 August–6 October and constituted 12% of wolf diet volume during this period (Table 1). We were not able to determine percent biomass for bear bait.

The mean weekly diet diversity index was 0.99 (range: 0.61–1.31). Diet diversity increased from June through October ($\hat{Y} = 0.737 + 0.033 * X$, $R^2 = 0.47$, $P < 0.01$, Fig. 2H). The mean

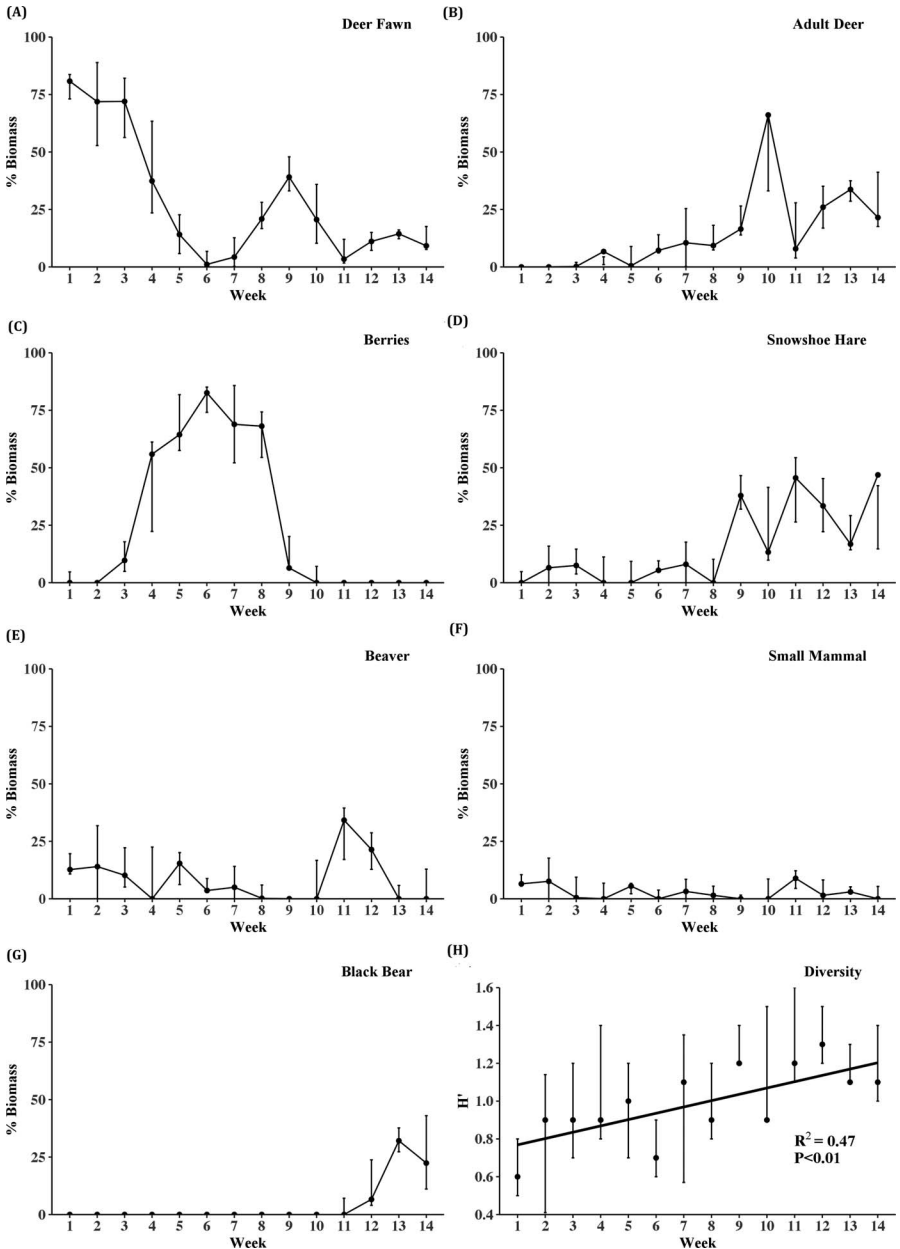


FIG. 2.—Percent of weekly wolf diet biomass composed of (A) deer fawns, (B) adult deer, (C) berries, (D) snowshoe hares (E) beaver, (F) small mammals, and (G) black bears as well as weekly diet diversity (H) in northeastern Minnesota based on scats collected from June 24 to October 6, 2015. Weekly diet diversity approximately doubled ($P < 0.05$) from June to October. After Week 10 adult deer and fawn hair was indistinguishable. Therefore, we estimated the percent volume and biomass of fawns and adults from Weeks 11–14 using the ratio seven adults: three fawns based on kill sites located in and around the study area. Week 14 includes scats from Week 15 due to small sample sizes

number of food types consumed per week was 4.4 (range: 3-6) and did not increase from June to October ($P = 0.38$). Every weekly biomass value of food types was within the 95% confidence intervals (CI) generated via simulations (Fig. 2) except for the 24 September–6 October point estimate for snowshoe hare, which exceeded the upper end of the 95% CI by 4.7%, suggesting our point estimate may have been slightly high or was merely a reflection of the high variability of wolf diet over short periods.

DISCUSSION

Ungulates typically constitute the majority of the diet of wolves with alternate prey such as beavers and hares making up the remainder (Peterson and Ciucci, 2003). However, during our 15 wk study nonungulate prey composed 58% of the diet of the Sheep Ranch Pack. Few examples exist where the majority of the diet of wolves is nonungulate prey (Peterson and Ciucci, 2003; Bosch *et al.* 2014), and in northern Minnesota ungulate prey typically constitutes 70–90% of the summer diet of wolves (Van Ballenberghe *et al.*, 1975; Fritts and Mech, 1981; Fuller, 1989; Chenaux-Ibrahim, 2015). When nonungulate prey is a substantial portion of summer wolf diets it is typically due to low ungulate densities or high densities of alternate prey (Chavez and Gese, 2005).

More strikingly, in mid to late summer this pack subsisted predominantly on blueberries. Indeed, berries were the second-most common food item (24% biomass) during our 15 wk study even though they were only available for 7 wk from early July to mid-August. Berries can be abundant during this time of year in boreal systems (up to 1.51 kg/m²; Usui *et al.*, 1994) but there are few examples in North America of wolves using berries or other fruits as a significant food source. In southern Quebec and northern Minnesota, berries occurred in 7–30% of summer scats (June 1–September 15) (Tremblay *et al.*, 2001) and 20–30% of scats at rendezvous sites during July–September, respectively (Van Ballenberghe *et al.*, 1975; Fuller, 1989). Fruit consumption has been more commonly observed in Europe, where fruits have been considered an important food item for wolves in some areas (Papageorgiou *et al.*, 1994; Peterson and Ciucci, 2003). In northern and western Italy, fruits composed 26% of annual diet volume and occurred in 60% of scats, respectively (Meriggi *et al.*, 1991, 1996).

Despite the abundance of berries in summer, there is an energetic trade-off for wolves when consuming berries instead of mammalian prey (Gable *et al.*, 2017b). Berries can have >3.75 times less energy (KJ/g dry wt) than mammalian prey (Usui *et al.*, 1994, Peterson and Ciucci, 2003). The digestibility of berries and other fruits is unknown but is likely low since wolves have a simple digestive tract evolved to digest animal protein (Mech, 1970; Andelt and Andelt, 1984). As a result wolves are likely losing weight when consuming large quantities of berries (Larivière *et al.*, 2001). However, during periods of reduced availability of vulnerable prey, berry consumption could be a way to minimize weight loss.

Deer fawn constituted a substantial proportion of weekly diet from late June to mid-July but then decreased abruptly in late July and by the first week of August only constituted 1% of weekly diet. This sharp decrease occurred when deer fawns were about 7 to 8 wk old (average parturition date of 26 May in Minnesota; Carstensen *et al.*, 2009), which is when fawns become capable of escaping canid predators (Nelson and Woolf, 1987). The dramatic decrease of deer fawn in the diet coincided with a similar increase of berries in the pack's weekly diet. Once blueberries were no longer available or abundant in our study area, there was an increase of deer fawns in weekly diet for a few weeks (13 August–2 September). However, this was not a functional response as the number of vulnerable fawns likely did not increase during this period. Instead, this likely reflects the stochastic nature of wolf hunting success. Predation events occur at irregular intervals as myriad factors affect wolves' ability to

locate and then kill vulnerable individuals (Mech and Peterson, 2003). Our results provide evidence of the variable hunting success of wolves when hunting both fawn and adult deer (*e.g.*, the sudden increase in adult deer in the diet during 27 August–2 September).

Nelson and Mech (1981) reported predation pressure on adult deer in other parts of northern Minnesota was low during the summer months. In our study predation on adult deer was low (<4% of the diet) until late summer (after mid-August) when adult deer became prevalent in the weekly diet (28% biomass). However, it is worth noting fawn and adult deer hair in wolf scats are indistinguishable by September. Although we estimated the proportion of fawn and adult deer after September using a fixed ratio (seven adults: three fawns) based on kill sites we investigated in and adjacent to the study area, this might not be representative of the true proportions of each consumed during a given week as the proportions of fawn and adult deer in weekly diet likely fluctuated with the pack's success in hunting fawns and/or adults during a given week.

Snowshoe hare were the primary food item from mid-August to early October. Snowshoe hares are typically an alternative prey item for wolves that make up a small percentage (<10%) of their diet (Theberge *et al.*, 1978; Fritts and Mech, 1981; Messier and Crête, 1985; Fuller, 1989; Forbes and Theberge, 1996). Although we do not have data on snowshoe hare densities, it is possible hares were abundant in the Sheep Ranch home range. Wolves can certainly capitalize on high hare densities (Mech, 1970), which might explain why snowshoe hares constituted 34% of mean weekly diet after 19 August.

The overall low consumption of beavers is curious because beavers were relatively abundant in the Sheep Ranch Pack's home range in 2015 (T. Gable, pers. obs.). Near the end of summer (3–16 September), wolf consumption of beavers increased to the largest observed beaver biomass values (21% and 34% biomass during 3–6 September and 10–16 September, respectively). Beavers are typically more vulnerable during September–October than during June–August as they are spending more time on land to obtain woody vegetation to either add to the lodge or to provision the food cache (Shelton, 1966; Hall, 1971; Gable *et al.*, 2016). Therefore, we would have expected consumption to continue into late September and early October when beavers spend an increasing amount of time on food cache construction and are especially vulnerable to predation (Buech, 1995). However, the presence of abundant available food from recreational black bear hunting could have led to the low consumption of beavers during this time.

The Sheep Ranch Pack quickly responded to the presence of bear bait piles as bear bait was 21% of wolf diet volume during 20 August–2 September. Many of the scats composed of bear bait had a paste-like consistency from masticated nuts and seeds with whole nuts and seeds present as well. Bear bait can consist of a variety of foods with many that are likely more digestible than nuts and seeds (*e.g.*, table scraps, fish carcasses, and rotting meat). Therefore, bear bait could provide an abundant energy-rich source of food during this time, and the collared Sheep Ranch wolf localized around bear bait piles in late August and early September (Gable, pers. obs.). Palacios and Mech (2010) documented a similar response with one instance where a collared wolf spent 161 h at an apparent bear bait pile of rotting meat.

In late September and early October, black bears were a significant food item for this wolf pack, which is likely the result of bears that had been either wounded or killed by hunters. Wolves rarely kill and consume black bears but wounded bears could be predisposed to wolf predation (Rogers and Mech, 1981). We believe it is more likely wolves scavenged gut piles from successfully harvested bears and carcasses of wounded bears, that died days or weeks after being shot. Similar behaviors have been reported in northeastern Minnesota and

central Ontario where wolves apparently scavenged carcasses of nuisance bears that were shot and killed near residential areas (Rogers and Mech, 1981). Cumulatively, food from black bear hunting composed a substantial amount of the Sheep Ranch Pack diet from mid-August to October.

The two-fold increase in diet diversity over the course of our 15 wk study highlights the plasticity of wolf foraging strategies. The number of food types consumed during our study fluctuated weekly but did not increase with time. Diet diversity was lowest in mid-summer when one food item (*e.g.*, berries or deer fawns) composed the majority of the diet. As expected weekly diet diversity was highest in late summer (Fig. 2) when neonatal deer fawns were no longer available but the energetic demand of pups remained high (Fuller *et al.*, 2003).

Monthly and seasonal diet analysis can identify large-scale patterns in wolf diets but can overlook fine-scale temporal shifts. Moreover, examining diet at these longer time scales can obscure the rapidity with which wolves can respond to the changing abundance of food types that are only available for short periods of time and the variable hunting success of wolves during this time of year. By examining weekly diet, we documented wolves responding to new available food sources in a matter of days. Dietary plasticity is undoubtedly advantageous as it allows wolves to persist in a variety of habitats with fluctuating prey availability and has likely contributed to the widespread distribution of wolves across North America, Europe, and Asia (Peterson and Ciucci, 2003).

Our results illustrate the fine-scale foraging patterns of a wolf pack in a human-modified landscape for a season. Future research should focus on fine-scale diets of other packs in different systems (both modified and unmodified) during different times of the year to examine whether wolves respond similarly to changing food availability or if wolves use other foraging strategies (*e.g.*, specializing on particular prey). Furthermore, it would be of interest to understand how foraging behavior and movements change during periods when wolves are primarily consuming nonmammalian foods. We expect dietary shifts towards nonmammalian foods would be reflected in wolf behavior, movement, and space-use. Additional research is needed to understand the caloric value of nonmammalian food types (*e.g.*, berries) because percent biomass or volume likely does not reflect the actual energetic contributions of these foods to wolf diets.

Acknowledgments.—We thank L. David Mech for reviewing a previous draft of this manuscript and providing helpful comments. We thank Voyageurs National Park, the National Park Service Great Lakes Research and Education Center, Northern Michigan University Wolf Park, Rainy Lake Conservancy, and the contributions of 58 individuals via a crowd-funding campaign for providing financial support for this project. We also thank A. Homkes and S. Johnson-Bice for assisting with the fieldwork for this project. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- ANDELT, W. F. AND S. H. ANDELT. 1984. Diet bias in scat deposition-rate surveys of coyote density. *Wildl. Soc. Bull.*, **12**:74–77.
- ANDHERIA, A. P., K. U. KARANTH, AND N. S. KUMAR. 2007. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *J. Zoo.*, **273**:169–175.
- BARBER-MEYER, S. AND L. D. MECH. 2015. Gray wolf (*Canis lupus*) dyad monthly association rates by demographic group. *Can. Wildl. Bio. Manage.*, **4**:163–168.
- BAILEY, R. G. 1980. Description of the ecoregions of the United States. U.S. Department of Agriculture, Miscellaneous Publication No. 1391, 77 p.
- BOSCH, G., E. A. HAGEN-PLANTINGA, AND W. H. HENDRIKS. 2014. Dietary nutrient profiles of wild wolves: insights for optimal dog nutrition? *Brit. J. Nutr.*, **113**:S40–S54.

- BUECH, R. R. 1995. Sex differences in behavior of beavers living in near-boreal lake habitat. *Can. J. Zool.*, **73**:2133–2143.
- BURSTHALER, C. M., J. D. ROTH, R. J. GAU, AND D. L. MURRAY. 2016. Demographic differences in diet breadth of Canada lynx during a fluctuation in prey availability. *Ecol. Evol.*, **6**:6366–6375.
- CARSTENSEN, M., G. D. DELGIUDICE, B. A. SAMPSON, AND D. W. KUEHN. 2009. Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. *J. Wildl. Manage.*, **73**:175–183.
- CHAVEZ, A. S. AND E. M. GESE. 2005. Food habits of wolves in relation to livestock depredations in Northwestern Minnesota. *Am. Mid. Nat.*, **154**:253–263.
- CHENAUX-IBRAHIM, Y. 2015. Seasonal diet composition of gray wolves (*Canis lupus*) in northeastern Minnesota determined by scat analysis. M.Sc. Thesis, University of Minnesota-Duluth, Duluth. 86 p.
- DARIMONT, C. T. AND T. E. REIMCHEN. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Can. J. Zool.*, **80**:1638–1642.
- DELL'ARTE, G. L., T. LAAKSONEN, K. NORRDAHL, AND E. KORPIMAKI. 2007. Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecol.*, **31**:276–281.
- FORBES, G. J. AND J. B. THEBERGE. 1996. Response by wolves to prey variation in central Ontario. *Can. J. Zool.*, **74**:1511–1520.
- FRITTS, S. H. AND L. D. MECH. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildl. Monogr.*, **80**:3–79.
- FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildl. Monogr.*, **105**:3–41.
- FULLER, T. K., L. D. MECH, AND J. F. COCHRANE. 2003. Wolf population dynamics, p. 161–191. In: L.D. Mech and L. Boitani (eds.). *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, Illinois. 448 p.
- GABLE, T. D. 2016. Wolf predation: where and how wolves hunt beavers, and confronting the biases in scat-based diet studies. M.Sc. Thesis, Northern Michigan University, Marquette. 71 p.
- , S. K. WINDELS, AND B. T. OLSON. 2017a. Estimates of white-tailed deer density in Voyageurs National Park: 1989–2016. Natural Resource Report NPS/VOYA/NRR—2017/1427. National Park Service, Fort Collins, Colorado.
- , ———, AND J. G. BRUGGINK. 2017b. Estimating biomass of berries consumed by gray wolves. *Wildl. Soc. Bull.*, **42**:528–531.
- , ———, AND ———. 2017c. The problems with pooling poop: confronting sampling method biases in scat-based wolf (*Canis lupus*) diet studies. *Can. J. Zool.* **95**: 843–851.
- , ———, ———, AND A. T. HOMKES. 2016. Where and how wolves (*Canis lupus*) kill beavers (*Castor canadensis*). *PLoS One*, **11**:e0165537.
- HALL, A. M. 1971. Ecology of beaver and selection of prey by wolves in central Ontario. M.Sc. Thesis, University of Toronto, Ontario. 124 p.
- JOHNSTON, C. A. AND S. K. WINDELS. 2015. Using beaver works to estimate colony activity in boreal landscapes. *J. Wildl. Manage.*, **79**:1072–1080.
- LARIVIÈRE, S., M. CRÈTE, J. HUOT, R. PATENAUDE, C. PRICE, AND D. W. THOMAS. 2001. Influence of food shortage during the summer on body composition and reproductive hormones in the red fox, *Vulpes vulpes*. *Can. J. Zool.*, **79**:471–477.
- LATHAM, A. D. M., M. C. LATHAM, K. H. KNOPFF, M. HEBBLEWHITE, AND S. BOUTIN. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography*, **36**:1276–1290.
- MECH, L. D. 1970. *The wolf: the ecology and behavior of an endangered species*. Natural History Press, Garden City, New York. 384 p.
- AND R. O. PETERSON. 2003. Wolf–prey relations, p.131–160. In L. D. Mech and L. Boitani (eds.). *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, Illinois. 448 p.
- , D. W. SMITH, AND D. R. MACNULTY. 2015. *Wolves on the hunt: the behavior of wolves hunting wild prey*. University of Chicago Press, Chicago, Illinois. 187 p.

- MERIGGI, A., A. BRANGI, C. MATTEUCCI, AND O. SACCHI. 1996. The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography*, **19**:287–295.
- , P. ROSA, A. BRANGI, AND C. MATTEUCCI. 1991. Habitat use and diet of the wolf in northern Italy. *Acta Theriologica*, **36**:141–151.
- MESSIER, F. AND M. CRÉTE. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia*, **65**:503–512.
- MILLS, K. J., B. R. PATTERSON, AND D. L. MURRAY. 2006. Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. *Wildl. Soc. Bull.*, **34**:1463–1469.
- NELSON, M. E. AND L. D. MECH. 1981. Deer social organization and wolf predation in northeastern Minnesota. *Wildl. Monogr.*, **77**:3–53.
- NELSON, T. A. AND A. WOOLF. 1987. Mortality of white-tailed deer fawns in southern Illinois. *J. Wildl. Manage.*, **51**:326–329.
- PAGE, M. L., J. J. COLE, S. R. CARPENTER, AND J. F. KITCHELL. 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, **14**:483–488.
- PALACIOS, V. AND L. D. MECH. 2010. Problems with studying wolf predation on small prey in summer via global positioning system collars. *Eur. J. Wildl. Res.*, **57**:149–156.
- PAPAGEORGIOU, N., C. VLACHOS, A. SFOUGARIS, AND E. TSACHALDIS. 1994. Status and diet of wolves in Greece. *Acta Theriologica*, **39**:411–416.
- PEERS, M. J. L., D. H. THORNTON, AND D. L. MURRAY. 2012. Reconsidering the specialist-generalist paradigm in niche breadth dynamics: resource gradient selection by Canada lynx and bobcat. *PLoS ONE*, **7**:e51488.
- PETERSON, R. O. AND P. CIUCCI. 2003. The wolf as a carnivore, p.104–130. *In*: L. D. Mech and L. Boitani (eds.). *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, Illinois. 448 p.
- PRUGH, L. R., S. M. ARTHUR, AND C. E. RITLAND. 2008. Use of faecal genotyping to determine individual diet. *Wildl. Bio.*, **14**:318–330.
- R CORE TEAM. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- ROGERS, L. L. AND L. D. MECH. 1981. Interactions of wolves and black bears in northeastern Minnesota. *J. Mammal.*, **62**:434–436.
- SHANNON, C. E. 1948. A mathematical theory of communication. *The Bell Sys. Tech. Journ.*, **27**:379–423, 623–656.
- SHELTON, P. C. 1966. Ecological studies of beavers, wolves, and moose in Isle Royale National Park, Michigan. Ph.D. Dissertation. Purdue University, Lafayette, Indiana. 307 p.
- SIDOROVICH, V. E., A. SCHNITZLER, C. SCHNITZLER, I. ROTENKO, AND Y. HOLIKAVA. 2017. Responses of wolf feeding habits after adverse climatic events in central-western Belarus. *Mamm. Bio.*, **83**:44–50.
- SIKES, R. S. and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.*, **92**:235–253.
- STANEK, A., N. WOLF, G. HILDERBRAND, B. MANGIPANE, D. CAUSEY, AND J. WELKER. 2017. Seasonal foraging strategies of Alaskan gray wolves (*Canis lupus*) in a salmon subsidized ecosystem. *Can. J. Zool.*, doi: 10.1139/cjz-2016-0203.
- STENGLEIN, J. L., L. P. WAITS, D. E. AUSBAND, C. M. MACK, AND P. ZAGER. 2010. Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. *J. Wildl. Manage.*, **74**:1050–1058.
- THEBERGE, J. B., S. M. OOSENBURG, AND D. H. PIMLOTT. 1978. Site and seasonal-variations in food of wolves, Algonquin Park, Ontario. *Can. Field. Nat.*, **92**:91–94.
- TREMBLAY, J. P., H. JOLICOEUR, AND R. LEMIEUX. 2001. Summer food habits of gray wolves in the boreal forest of the Lac Jacques-Cartier highlands, Québec. *Alces*, **37**:1–12.
- TRITES, A. W. AND R. JOY. 2005. Dietary analysis from fecal samples: how many scats are enough? *J. Mammal.*, **86**:704–712.
- USUI, M., P. G. KEVAN, AND Y. KAKUDA. 1994. Composition and energy values of wild fruits from the boreal forest of northern Ontario. *Can. J. Pla. Sci.*, **74**:281–287.

- VAN BALLEMBERGHE, V., A. W. ERICKSON, AND D. BYMAN. 1975. Ecology of the timber wolf in northeastern Minnesota. *Wildl. Monogr.*, **43**:3–43.
- VILLEPIQUE, J. T., B. M. PIERCE, V. C. BLEICH, AND R. T. BOWYER. 2011. Diet of cougars (*Puma concolor*) following a decline in a population of mule deer (*Odocoileus hemionus*): lack of evidence for switching prey. *Southwest Nat.*, **56**:187–192.
- WATTS, D. E. AND S. D. NEWSOME. 2017. Exploitation of marine resources by wolves in southwestern Alaska. *J. Mammal.*, **98**:66–76.
- WEAVER, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. *J. Wildl. Manage.*, **57**:534–538.
- AND S. H. FRITTS. 1979. Comparison of coyote and wolf scat diameters. *J. Wildl. Manage.*, **43**:786–788.
- WIEBE, N., G. SAMELIUS, R. T. ALISAUSKAS, J. L. BANTLE, C. BERGMAN, R. DE CARLE, C. J. HENDRICKSON, A. LUSIGNAN, K. J. PHIPPS, AND J. PITT. 2009. Foraging behaviours and diets of wolves in the Queen Maud Gulf Bird Sanctuary, Nunavut, Canada. *Arctic*, **62**:399–404.
- WINDELS, S. K. 2014. 2014 Voyageurs National Park moose population survey report. Natural Resource Data Series NPS/VOYA/NRDS—2014/645. National Park Service, Fort Collins, Colorado. 20 p.

SUBMITTED 14 NOVEMBER 2016

ACCEPTED 15 SEPTEMBER 2017