Temporal variation in translocated Isle Royale wolf diet reflects optimal foraging.

Adia Sovie[1], Mark Romanski[2], Elizabeth Orning[3], David Mareweck[4], Rachel Nichols[5], Seth Moore[5], and Jerrold Belant[1]

[1]Michigan State University
[2]Isle Royale National Park
[3]SUNY-ESF
[4]Conservation Alpha
[5]Grand Portage Band of Lake Superior Chippewa

August 24, 2022

Abstract

Wolves (Canis lupus) can exert top-down pressure and shape ecological communities through selective predation of ungulates and beavers (Castor Canadensis). Considering their ability to shape communities through predation, understanding wolf foraging decisions is critical to predicting their ecosystem level effects. Specifically, if wolves are optimal foragers, consumers that optimize tradeoffs between cost and benefits of prey acquisition, changes in these factors may lead to prey switching or negative-density dependent selection with potential consequences for community stability. For wolves, factors affecting cost and benefits include prey vulnerability, risk, reward, and availability which can vary temporally. We described wolf diet in by frequency of occurrence and percent biomass and characterized diet in relation to optimal foraging using prey remains found in wolf scats on Isle Royale National Park, Michigan, USA during May–October 2019–2020. We used logistic regression to estimate prey consumption over time. We predicted prey with temporal variation in cost (vulnerability and/or availability) such as adult and calf moose (Alces alces) and beaver to vary in wolves' diet. We analyzed 206 scats and identified 62% of remains as beaver, 26% as and moose, and 12% as other (birds, smaller mammals, and wolves). Adult moose were more likely to occur in wolf scat in May, when moose are in poor condition following winter. Similarly, the occurrence of moose calves peaked June–mid July following parturition but before their vulnerability declined as they matured. In contrast, beaver occurrence in wolf scat did not change over time, possibly reflecting the importance of low handling cost prey items for recently introduced lone or paired wolves. Our results demonstrate that wolf diet is plastic and responsive to temporal changes in prey acquisition cost as predicted by optimal foraging theory. Temporal fluctuation in diet may influence wolves' ecological role if prey respond to increased predation risk by altering their foraging or breeding behavior.

Temporal variation in translocated Isle Royale wolf diet reflects optimal foraging.

Adia R. Sovie[1], Mark C. Romanski[2], Elizabeth K. Orning[3], David G. Marneweck,[3,4], Rachel Nichols[3], Seth Moore[5], Jerrold L. Belant[1]

[1] Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, East Lansing, MI 48824, USA

[2] National Park Service, 800 E Lakeshore Drive, Isle Royale National Park, Houghton, MI 49931 USA

[3] State University of New York, College of Environmental Science and Forestry. 1 Forest Drive, Syracuse, NY 13210

[4] Conservation Alpha, Johannesburg, South Africa

[5]Department of Biology and Environment, Grand Portage Band of Lake Superior Chippewa, 27 Store Rd,
Grand Portage, MN 55605 USA

Abstract

Wolves (*Canis lupus*) can exert top-down pressure and shape ecological communities through selective predation of ungulates and beavers (*Castor canadensis*). Considering their ability to shape communities through predation, understanding wolf foraging decisions is critical to predicting their ecosystem level effects. Specifically, if wolves are optimal foragers, consumers that optimize tradeoffs between cost and benefits of prey acquisition, changes in these factors may lead to prey switching or negative-density dependent selection with potential consequences for community stability. For wolves, factors affecting cost and benefits include prey vulnerability, risk, reward, and availability which can vary temporally. We described wolf diet in by frequency of occurrence and percent biomass and characterized diet in relation to optimal foraging using prey remains found in wolf scats on Isle Royale National Park, Michigan, USA during May–October 2019–2020. We used logistic regression to estimate prey consumption over time. We predicted prey with temporal variation in cost (vulnerability and/or availability) such as adult and calf moose (*Alces alces*) and beaver to vary in wolves' diet. We analyzed 206 scats and identified 62% of remains as beaver, 26% as and moose, and 12% as other (birds, smaller mammals, and wolves). Adult moose were more likely to occur in wolf scat in May, when moose are in poor condition following winter. Similarly, the occurrence of moose calves peaked June–mid July following parturition but before their vulnerability declined as they matured. In contrast, beaver occurrence in wolf scat did not change over time, possibly reflecting the importance of low handling cost prey items for recently introduced lone or paired wolves. Our results demonstrate that wolf diet is plastic and responsive to temporal changes in prey acquisition cost as predicted by optimal foraging theory. Temporal fluctuation in diet may influence wolves' ecological role if prey respond to increased predation risk by altering their foraging or breeding behavior.

Keywords: Optimal foraging, Isle Royale, beaver, moose, wolf, diet

Introduction

Predation can shape ecosystems through controlling prey population abundance and influencing where prey forage, resulting in landscape scale changes to vegetation and nutrient flows (Terborgh *et al.* , 2001; Halpern *et al.* , 2006; Estes *et al.* , 2011). Specifically, wolf (*Canis lupus*) predation can produce strong top-down structuring in many systems (Bump *et al.,* 2009; Ripple and Beschta, 2012). While wolf predation can influence prey activity (Suraci *et al.* , 2016; Kohl et al 2018; Gaynor *et al.* , 2019), it is less clear if wolves are optimal foragers or if prey demography and behavior can drive wolf foraging decisions (Abrams, 1992; Katz *et al.* , 2015). Under optimal foraging theory, consumers optimize caloric intake by balancing the calories gained from a food item and the caloric and safety costs of searching for and handling the item (Pyke *et al.* , 1977). For wolves, the caloric benefits of prey items are relatively stable while the costs associated with acquisition [search time, subjugation difficulty, and risk of injury] change temporally. If wolves are optimal foragers, foraging patterns may change over time, resulting in prey switching with the potential for cascading ecological effects (Garrott *et al.* , 2007; Latham *et al.* , 2013; Basille *et al.* , 2013).

For wolves, the cost of prey acquisition includes search and handling time as well as injury risk, factors that can change over weeks or months (Griffiths, 1980; Mukherjee and Heithaus, 2013). Predators often target abundant prey to reduce the caloric costs associated with search time (Griffiths, 1980). The availability of prey can change temporally as species migrate into or out of a feeding range, emerge from hibernation or torpor, or following a birth pulse (Metz *et al.* , 2012; Petroelje *et al.* , 2014). Wolves do not always preferentially attack the most abundant prey, vulnerability and risk are also factors driving wolf foraging decisions (Mech & Peterson 2003; Tallian *et al.* , 2017; Hoy *et al.* , 2021). Larger animals require greater effort and risk to subdue (Griffiths 1980; MacNulty*et al.* , 2009). In contrast, smaller animals or prey in poor condition exhaust quicker, require less effort to subdue, and are less likely to inflict injuries (MacNulty *et al.* , 2009; Krumm *et al.* , 2010). Prey risk and vulnerability change temporally (Metz et al 2012). For example, ungulates are often nutritionally deficient after winter (Huggard 1993; Kautz *et al.* , 2020) and young animals develop the speed and endurance necessary to evade capture as they mature (Severud *et al.* , 2019). If wolves are optimal foragers these temporal shifts in prey demography and behavior may alter wolf diet.

Recently reintroduced wolves on Isle Royale National Park (IRNP), Michigan, USA provide a unique opportunity to investigate wolf diet relative to optimal foraging theory. Wolves on IRNP prey on a limited number of species that predictably vary in caloric value, availability, and vulnerability, allowing us to evaluate hypotheses of optimal foraging and prey switching. During the ice-free season (April–October) wolves in IRNP historically preyed on moose and beavers but also consumed snowshoe hare (*Lepus americanus)* , small mammals, and birds (Thurber and Peterson, 1993). Wolves in IRNP consume 4-7kg/wolf of biomass a day (Thurber and Peterson, 1993), and should select for large prey to maximize caloric intake (Carbone *et al.* , 1999). Adult moose (263 kg) are a high calorie prey item but require considerable effort to locate and subdue (Sand *et al.* , 2005). Adult moose are most vulnerable in May due to winter malnutrition but regain fat reserves after green-up in June and July (Parker, 2003; Tischler*et al.* , 2019). In contrast, moose calves (45kg) are not as calorically rewarding as adults but require less handling time and risk (Hoy *et al.* , 2021). Calves are unavailable until parturition in late May and are guarded by their mothers for the first few weeks of their lives (Edwards, 1983; Stephens and Peterson, 1984). Moose calves are most vulnerable to wolf attack in late June and into July, as they spend less time with their mothers, but are capable of outrunning wolves by September (Severud *et al.* , 2019). Beavers (12 kg) are a low risk and abundant food source on IRNP during the ice-free season. In May following ice-out and in September before ponds freeze, beavers are vulnerable to wolf predation when they forage on land to repair lodges or restore food caches (Gable *et al.* , 2017).

We estimated wolf diets from scats in IRNP in relation to optimal foraging during the ice-free period 2019–2020. We hypothesized that wolf diets would reflect an optimal foraging strategy that tracks temporal shifts in prey acquisitions costs. Specifically, we predicted that due to their high caloric value moose would be the primary component of wolf diet by both frequency of occurrence and biomass in scats. We also predicted the presence of moose in the wolf diet will be highest in May and decline thereafter. Further, we predicted that moose calf occurrence in scats would follow a nonlinear relationship, peaking in late-June after parturition and declining in late summer as calves grow and become less vulnerable to wolf predation. We predicted that beaver occurrence in wolf diets would vary with peaks in May and September. Finally, we predicted that other prey (e.g., snowshoe hares, small mammals, and birds) would increase in occurrence in late summer as moose become more difficult to kill and wolves increase their use of alternative prey (Gable *et al.* , 2018).

Methods

Study Area

Isle Royale National Park is a 540-km^2 archipelago in Lake Superior, 22 km from mainland Ontario, Canada. Over 99% of the park is designated wilderness and supports mixed boreal forests characteristic of the transition between temperate and boreal zones (Sanders and Grochowski, 2013). Mammals on Isle Royale include moose, wolves, red foxes (*Vulpes vulpes*), beavers, river otter (*Lontra canadensis*), snowshoe hare, red squirrels (*Tamiasciurus hudsonicus*), muskrats (*Ondatra zibethicus*), deer mice (*Peromyscus maniculatus),* and several species of bats (Johnsson *et al* ., 1982). Mean daily high temperatures in summer (June–August) are 21°C and mean daily high temperatures in winter (December–February) are 3°C. Isle Royale receives an average of 734 mm in annual precipitation.

Isle Royale National Park personnel and partner organizations released 19 wolves into IRNP in 2018 and 2019 to supplement the population. Eight of these wolves represented a family group from Michipicoten Island, Ontario and the remaining wolves were unassociated and unrelated individuals (Hervey *et al.* , 2021). Before restoration, only two highly inbreed wolves remained on the island (Hervey *et al.* , 2021). All translocated wolves received Vectronics or Telonics radio-collars with on-board Global Positioning System (GPS) scheduled to take a location every 5 hours (NPS, unpublished data).

Scat Collection and Processing

From 5 May–5 October 2019 and 13 June–22 September 2020, we collected all wolf scats encountered during fieldwork in IRNP. We collected fresh scats (e.g., strong smell, moist, tracks present) at wolf radio-collar GPS location clusters (Svoboda *et al.* , 2013) and on established hiking trails (Fig. 1). We placed each scat in a plastic bag, recorded the date and location (NAD83, UTM Zone 16N), and froze them for later processing. We considered the collection date as the date of deposit, although scats may have been up to 11 days old (Sanchez *et al.* , 2004).

We processed and identified scat contents following Chenaux–Ibrahim (2015). We placed frozen scats into nylon stockings, washed them in a washing machine to remove digestible material and then dried the contents in an oven. We spread the contents on a 21.5cm x 28cm plate, overlaid a 25-point grid, and randomly selected one hair from each point for microscopic identification (Ciucci *et al* ., 2004). We could determine moose age class (adult or calf) until 15 September, when the first molt occurs (Muller, 2006). After 15 September we identified all moose hair as adult. Wolf hair may be ingested due to grooming or cannibalistic activity, the latter resulting in a higher amount of hair in scats (James, 1983; Muller, 2006). Therefore, we did not consider wolf as a prey item unless we detected wolf hair at >10% of points in a sample. We pooled all other prey (birds, muskrats, small mammals, wolves, unidentifiable remains, and vegetation) into an "other" category.

Prey Occurrence and Biomass

For each scat we calculated frequency of occurrence (FO) and percent biomass of each prey item (Mech, 1966; Thurber and Peterson, 1993). We calculated FO as the total number of occurrences on the point grid divided by the total number of points in the sample. As FO can overrepresent small prey and younger animals, we also calculated the percent biomass ingested (Floyd *et al.* , 1978; Ciucci *et al.* , 1996; Klare *et al.* , 2011). To calculate biomass for each species we multiplied the number of occurrences on the point frame by a correction factor y = 0.439 + 0.008 * x, where x is the live mass of the prey item (Floyd *et al.* , 1978). We used the live mass of adult moose, calf moose, and beavers on Isle Royale (Thurber and Peterson, 1993). Due to identification uncertainty, we did not calculate the biomass contribution of species categorized as "other".

We used logistic regression to estimate temporal variation in wolf diet. For each scat we recorded presence/absence for each prey species and built models representing our hypothesis of how wolf diet may change over time. For each species we built three models with species/presence absence as the response and constant, linear, or non–linear time as predictors. We considered coefficients from models informative when the 95% confidence interval around the beta estimate did not overlap 0. We used Akaike Information Criterion corrected for small samples (AICc) and AICc weight to select the most parsimonious model (Burnham and Anderson, 2002). We considered models within two AICc units of the best model as competing models unless they we more complex than the top model and the coefficients of the additional variables were not informative (Burnham and Anderson, 2002).

Due to difficulty identifying moose to age class after September 15 we ran two sets of models for each statistical approach. The first included all scats with all moose pooled and the second set included scats collected 5 May–15 September with moose separated by age class.

Results

We collected 206 scats, 126 in 2019 and 90 in 2020, and detected seven prey items (Table 1). Scats on average contained 1.6 + 0.8 standard deviation [SD] items per scat with 56% containing 1 item. We did not detect a difference in prey occurrence in scats between years ($\beta_{\mathrm{Mooseyear}}$ =-0.15, se=0.28; $\beta_{\mathrm{Beaveryear}}$=-0.09, se=0.34; $\beta_{\mathrm{Otheryear}}$=0.26, se=0.34) so we pooled all samples for further analysis. The most frequent prey overall in wolf scats was beaver (62%), followed by moose (26%), and other prey (11%; Fig. 2). When we pooled moose age classes, moose comprised 61% of biomass ingested and beaver 39% (Fig. 2A). In scats collected 5 May–15 September, beaver remained the most common prey item (66%), followed by adult moose (15%), calf moose (10%), and other prey (8%) (Fig. 2B). From this subset of scats, beaver and adult moose were the most important prey items by biomass (47% and 42% respectively), while moose calves represented 10% of the wolf diet. Wolf was rare in samples, with only one scat comprised entirely of wolf hair (100% of points in the frame).

Using all scats combined, the linear time model was the most parsimonious for moose and other prey (Table 2). While non-linear time models were supported by the data, the additional parameters were not informative (Sup 1). The probability of moose hair occurrence declined (β_{Time} = -0.31, se = 0.03) from 0.66 in May to 0.36 in October (Fig. 3A). The probability of other prey items occurring in scat increased (β_{Time} = 0.41, se = 0.19) from 0.09 in May to 0.33 in October (Fig. 3A). The most parsimonious model for beaver was constant over time, with the overall probability of occurrence in wolf scat 0.78 (95% CI = 0.72–0.84) (Fig. 3A). A linear time models was supported by the data but the additional parameter did not improve parsimony and was not informative (Sup 1).

When considering moose by age class, 5 May–15 September, the most parsimonious model for adult moose was constant over time. The probability of adult moose hair in scat was 0.30 (95% CI = 0.23–0.37) (Table 3, Fig. 3B). In contrast, the best model for the presence of calf hair in scats was nonlinear, with the probability of calf hair greatest in the first week of July (0.44, 95% CI = 0.30–0.58) and declining through mid-September (β_{Time} = 7.11, se = 2.58; ${\beta_{\text{Time}}}^2$ = -7.75, se = 2.65).

Discussion

We found that wolf foraging decisions in IRNP are likely influenced by the population dynamics and vulnerability of their prey. As predicted under optimal foraging theory, wolves on Isle Royale shifted their diet in response to prey vulnerability and availability. Viewing wolf diet in relation to optimal foraging can explain why the diet of wolves in IRNP diverged from previous studies. In North America and Europe large and medium-size ungulates comprise >60% of wolf diet by frequency of occurrence (Carbone *et al.* , 1999; Theuerkauf 2009; Derbridge *et al.* , 2012; Newsome *et al* ., 2016). In contrast, in IRNP ungulates comprised only 26% of the wolf diet by FO. Our findings likely reflect the relative availability and vulnerability of moose and beaver in IRNP. Beavers in IRNP are at historically high densities of >1 colony/km^2 (NPS unpublished data; Smith and Peterson, 2021) and wolves can ambush and subdue beavers in less than 5 minutes (Gable *at al.* , 2018). In contrast, moose density (˜3.7/km2) in IRNP is within its historic [1960–2020] range (Smith and Peterson, 2021). Also, wolves often exert considerable energy to subdue moose, chasing them up to 1 km (Mech, 1966; Paquet, 1989). While moose are an order of magnitude more calorically profitable than beavers, the abundance and ease of capture of beavers (Mech *et al.* , 2015) makes them an important prey of wolves in IRNP. Thus, aligning with optimal foraging theory, wolves on IRNP appear to select prey (i.e. beavers) that are highly available (benefit) and easier to catch (lower costs) than larger ungulates (i.e. moose).

Contrary to our prediction that beaver would be an important secondary and temporally variable food item, wolves on Isle Royale consumed beaver at high rates throughout the ice-free season. The high amount of beaver consumption we observed is atypical for IRNP (Thurber and Peterson, 1993) and wolves in general (Newsome *et al.* , 2016) and likely reflects high beaver availability and vulnerability in conjunction with weak wolf pack formation. Beaver densities appear to be at historic high levels with 1 colony/km^2 (Smith and Peterson, 2021) compared with a mean of 0.28 colony/km^2 from 1962–2008 when beaver comprised only 14% of biomass of the wolf diet in IRNP (Romanski, 2010; Gable *et al.* , 2017). High beaver densities likely reduce wolf search time and may increase beaver vulnerability as they forage farther from water as palatable trees near ponds become limited (Gable *at al.* , 2018). In addition, approximately half of the wolves in IRNP were not associated with a pack during our study (NPS unpublished data), and smaller prey may be less risky for solo or small packs of wolves to attack (Escobedo *et al* ., 2015).

While beavers were the most frequently consumed prey item, moose contributed 50% more biomass to the wolf diet. Moose comprised most of the biomass ingested by wolves, which supported our predictions, however, moose comprised less of the wolf diet than we expected. In the Great Lakes Region of North America, ungulates comprise >80% of the wolf diet and historically (1975–1989) 85–95% of biomass consumed by

IRNP wolves (Thurber and Peterson, 1993; Newsome *et al.* , 2016). This shift in wolf diet may be a result of high beaver density, moose age class structure, or lack of pack formation. Prey age structure can impact wolf kill rates (Sand *et al.* , 2012) as moose calves and adults $>$ 6 years old are most vulnerable to wolf predation. Our temporal analyses highlight the importance of available vulnerable moose (i.e. nutritionally deficient adults in early spring and calves after parturition) and a lack of vulnerable moose may skew the wolf diet on IRNP. Further, the likely limited pack cohesion in recently introduced wolves (NPS unpublished data) may account for the low occurrence of moose in the diet. Cooperative hunting increases the efficiency of capturing larger prey, and there is a positive correlation between group size and prey size among social carnivores (Macdonald, 1983; MacNulty *et al* ., 2014). While paired and single wolves can kill moose (Thurber and Peterson, 1993), increased pack size can improve wolf success rate for difficult to capture prey (MacNulty *et al.* , 2014). For paired or single wolves, hunting beaver in IRNP is less risky and potentially as energetically efficient as hunting moose.

In accordance with our predictions, adult moose were more likely to occur in wolf scat early in the ice-free season, consistent with previous studies demonstrating the importance of individuals in poor condition in the wolf diet (Stahler *et al.* , 2006; Hoy *et al.* , 2021). In addition, the prevalence of moose in the wolf diet early in the ice-free season may indicate the importance of scavenging starving or winter tick (*Dermacentor albipictus*) infested individuals (Forbes and Theberge, 1992). Our results suggest that scavenging may be a common early summer strategy in wolf-moose systems (Messier and Crete, 1985; Forbes and Theberge, 1992; Huggard, 1993; Orning *et al.* , 2021).

The occurrence of moose calf hair in wolf scats peaked in late-June, as predicted under optimal foraging theory. However, moose calves made up less of the wolf diet than we expected with calves comprising 10% of the biomass ingested, similar to rates reported by Thurber and Peterson (1993). This amount of consumption of calves is low for wolves, which tend to select for juvenile ungulates (Husseman *et al* ., 2003; Mattioli *et al.* , 2011) and calves can comprise 60–90% of biomass ingested in some moose-wolf systems (Wam and Hjeljord 2003; Sand*et al.* , 2008). Possibly, increased cow vigilance on IRNP (Edwards, 1983; Stephens and Peterson, 1984), may result in a shorter period of calf vulnerability than in other systems, reducing the importance of calves in the wolf ice-free diet. Interestingly, our results differ from Hoy *et al.* (2021) who reported strong, negative-frequency dependent selection for moose calves by IRNP wolves in winter. This divergence in summer/winter feeding may be a result of the larger prey base available to wolves in the ice-free season. Possibly, the availability and vulnerability of beaver may alleviate predation pressure on moose calves at low densities.

As moose became more difficult to capture the occurrence of less calorically valuable items (snowshoe hare, small mammals and birds, categorized as "other") increased in wolf scats. Our results highlight the importance of alternative prey in supporting wolves through resource limited periods. Prey switching can allow higher densities of wolves to persist on a landscape as well as alter the population and behavior of secondary prey (Garrot *et al.* , 2007; Latham, 2013). Snowshoe hare act as an important herbivore on Isle Royale (Belovsky, 1984) and increased wolf predation of hares in late summer may help limit the effects of hare browsing on vegetation.

Our results may be limited by the inherent difficulty of estimating predator diets in forested landscapes. Scat analysis provides strong advantages over tracking or GPS cluster investigation to document small or rare items in the wolf diet (Klare et al., 2011). However, scat analysis is prone to observer error, can over-represent small prey, assumes constant scat deposition rates, and biomass calculations rely on strong assumptions of carcass use (Spaulding *et al* ., 2000; Klare*at al.* , 2011; Massey *et al.* , 2021). Specifically, in IRNP wolves often scavenge and/or partially consume carcasses (see Vucetich*et al.* , 2011), which could bias our biomass calculations. Also, due to the difficulty of identifying moose calves after the first molt, we assumed all moose hair in scats after September 15th were from adults. This assumption may inflate the biomass of moose consumed after 15 September as these could include young of the year post molt. Finally, because of our opportunistic scat collection, some individuals may be overrepresented (i.e. radio collared wolves and their pack members). However, our study was unique in that all but two wolves in IRNP were radio collared at the time of our study and contributed to GPS clusters, increasing the probability that we sampled the entire population.

Wolves appear to optimize tradeoffs between the costs and benefits of prey acquisition temporally, dynamically responding to changes over time. Just as prey respond to seasonal variability in predation risk, we found wolves responded to seasonal changes in prey availability and vulnerability (Garrott *et al.* , 2007; Latham *et al.* , 2013; Basille *et al.* , 2013). The tendency of wolves to prey switch in response to changes in prey availability is unclear, with some studies indicating negative-frequency dependence (Tallian et al., 2017; Hoy*et al.* , 2021) and other studies suggesting prey-switching (Garrott *et al.* , 2007; Latham et al., 2013). We found that wolves appeared to shift their diet in response to prey availability and vulnerability, supporting the prey switching hypothesis. The dynamic summer foraging behavior of wolves may have important cascading and landscape consequences. Specifically, the high rate of beaver predation may restore ecological function and influence landscape-level change in IRNP. Beavers are at historically high densities in IRNP, and the wetlands they create can dramatically alter landscape–level water and nutrient flow (Rosell 2005). Wolf predation could reduce the number and duration of these impoundments (Gable *et al.* , 2020) and restore interrupted ecological functions in these areas. Further, the relatively low occurrence of moose in the wolf diet may indicate that, when vulnerable alternative prey are available, wolves may not exert top-down regulation on moose populations. Our results support that wolves are dynamic optimal foragers and their ability to shape ecosystems is likely dependent on the behavior and demography of their prey.

Acknowledgements

This project was supported by the US National Park Service. M. Cooper, H. Boone, L. McTigue, M. Petersohn, J. Olson, C. Ratterman, and T. Schwelling collected field samples.

Author Contributions

Adia Sovie: Writing – original draft (equal); formal analysis (lead); writing – review and editing (equal). **Mark Romanski** : Conceptualization (equal); funding acquisition (lead); writing – review and editing (equal). **Elizabeth Orning** : Methodology (lead); investigation (lead); writing – review and editing (equal). . **David G. Marneweck** : Investigation (supporting); writing – review and editing (equal). **Rachel Nichols** : Investigation (supporting); writing – review and editing (supporting). Seth Moore: Resources (lead). Jerrold Belant: Conceptualization (equal); supervision (lead); writing – original draft (equal) ; writing – review and editing (equal).

Works Cited

Abrams, P.A. 1992. Adaptive foraging by predators as a cause of predator-prey cycles. *Evolutionary Ecology* , **6** :56–72.

Basille, M., D. Fortin, C. Dussault, J.P. Ouellet, and R. Courtois. 2013. Ecologically based definition of seasons clarifies predator–prey interactions. *Ecography* , **36** :220–229.

Belovsky, G.E. 1984. Herbivore optimal foraging: a comparative test of three models. *The American Naturalist* , **124** :97-115.

Beschta, R.L., and W.J. Ripple. 2019. Can large carnivores change streams via a trophic cascade? *Ecohydrology* , **12** :2048.

Bump, J.K., R.O. Peterson, and J.A. Vucetich. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecology* , **90** :3159–3167.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd Edition, Springer-Verlag, New York.

Carbone, C., Mace, G.M., Roberts, S.C. and Macdonald, D.W. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* , 402(6759):286-288.

Chenaux-Ibrahim, Y., 2015. Seasonal diet composition of gray wolves (Canis lupus) in northeastern Minnesota determined by scat analysis (Doctoral dissertation, University of Minnesota).

Ciucci, P., E. Tosoni, and L. Boitani. 2004. Assessment of the point-frame method to quantify wolf (*Canis lupus*) diet by scat analysis. *Wildlife Biology* , **10** :149-153

Ciucci, P., L. Boitani, E.R. Pelliccioni, M. Roco, and I. Guy. 1996. A comparison of scat analysis methods to assess the diet of the wolf (*Canis lupus*). *Wildlife Biology* , **1** :37-48.

Derbridge, J.J., P.R. Krausman, and C.T. Darimont. 2012. Using Bayesian stable isotope mixing models to estimate wolf diet in a multi-prey ecosystem. *The Journal of Wildlife Management* , **76** :1277-1289.

Edwards, J. 1983. Diet shifts in moose due to predator avoidance.*Oecologia,* **60** :185–189

Escobedo, R., Dutykh, D., Muro, C., Spector, L. and Coppinger, R. 2015. Group size effect on the success of wolves hunting. arXiv preprint arXiv:1508.00684.

Estes, J.A., J. Terborgh, J.S. Brashares, M.E. Power, J. Berger, W.J. Bond, S.R. Carpenter, T.E. Essington, R.D. Holt, J.B. Jackson, and R.J. Marquis. 2011. Trophic downgrading of planet Earth. *Science* , **333** :301–306.

Floyd, T.J., L.D. Mech, and P.A. Jordan. 1978. Relating wolf scat content to prey consumed. *The Journal of Wildlife Management* ,**45** :528–532.

Forbes, G.J., and J.B. Theberge. 1992. Importance of scavenging on moose by wolves in Algonquin Park, Ontario. *Alces* , **28** :235-241.

Gable, T.D. and S.K. Windels. 2018. Kill rates and predation rates of wolves on beavers. *The Journal of Wildlife Management* , **82** :466–472.

Gable, T.D., S.K. Windels, and J.G. Bruggink. 2017. The problems with pooling poop: confronting sampling method biases in wolf (*Canis lupus*) diet studies. *Canadian Journal of Zoology* , **95** :843–851.

Gable, T.D., S.K. Windels, J.G. Bruggink, and S.M. Barber-Meyer. 2018. Weekly summer diet of gray wolves (*Canis lupus*) in northeastern Minnesota. *The American Midland Naturalist* , **179** :15–27.

Gable, T.D., S.M. Johnson-Bice, A.T. Homkes, S.K. Windels, and J.K Bump. 2020. Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. *Science Advances* , **6** :5439.

Gable, T.D., T. Stanger, S.K. Windels, and Bump J.K. 2018. Do wolves ambush beavers? Video evidence for higher-order hunting strategies. *Ecosphere* , **9** :02159.

Garrott, R.A., J.E. Bruggeman, M.S. Becker, S.T. Kalinowski, and P.J. White. 2007. Evaluating prey switching in wolf-ungulate systems. *Ecological Applications* , **17** :1588–1597.

Gaynor, K.M., J.S. Brown, A.D. Middleton, M.E. Power, and J.S. Brashares. 2019. Landscapes of fear: spatial patterns of risk perception and response. *Trends in Ecology and Evolution* , **34** :355–368.

Griffiths, D. 1980. Foraging costs and relative prey size. *The American Naturalist* , **116** :743–752.

Halpern, B.S., K. Cottenie, and B.R. Broitman, 2006. Strong top-down control in southern California kelp forest ecosystems. *Science* , **312** :1230-1232.

Hervey, S.D., Rutledge, L.Y., Patterson, B.R., Romanski, M.C., Vucetich, J.A., Belant, J.L., Beyer, D.E., Moore, S.A. and Brzeski, K.E. 2021. A first genetic assessment of the newly introduced Isle Royale gray wolves (*Canis lupus*). *Conservation Genetics* , **22** (6):913-926.

Hoy, S.R., D.R. MacNulty, M.C. Metz, D.W. Smith, D.R. Stahler, R.O. Peterson, J.A. Vucetich. 2021. Negative frequency–dependent prey selection by wolves and its implications on predator-prey dynamics. *Animal Behaviour* , **179** :247–265.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. *Canadian Journal of Zoology* ,**71** :140– 147.

Husseman, J.S., D.L. Murray, G. Power, C. Mack, C.R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* , **101** :591-601.

James, D.D. 1983. Seasonal movements, summer food habits, and summer predation rates of wolves in northwest Alaska. Doctoral dissertation, University of Alaska, Fairbanks.

Johnsson R., P. Shelton, P. Jordan. 1982. Wildlife of Isle Royale: checklists of all vertebrate animals known at Isle Royale including their current status. Isle Royale Natural History Association.

Katz, M.W., Z. Abramsky, B.P. Kotler, I. Roth, S. Livne, O. Altstein, and M.L Rosenzweig. 2015. A predator-prey foraging game: how does prey density influence tactics?. *Evolutionary Ecology Research* , **16** :323–335.

Kautz, T.M., J.L. Belant, D.E. Beyer, B.K. Strickland, and J.F. Duquette. 2020. Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: Evidence for a late-winter survival bottleneck. *Ecology and Evolution* , **10** :1666–1677.

Klare, U., J.F. Kamler, and D.W. Macdonald. 2011. A comparison and critique of different scat–analysis methods for determining carnivore diet. *Mammal Review* , **41** :294–312.

Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., White, P.J., Smith, D.W. and MacNulty, D.R. 2018. Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* , **88** (4):638-652.

Krumm, C.E., M.M. Conner, N.T. Hobbs, D.O. Hunter, and M.W. Miller. 2010. Mountain lions prey selectively on prion-infected mule deer. *Biology Letters* , **6** :209–211.

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.

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature* , **301** :379–384.

MacNulty, D.R., A. Tallian, D.R. Stahler, and D.W. Smith. 2014. Influence of group size on the success of wolves hunting bison. *PloS one* , **9** :112884.

MacNulty, D.R., D.W. Smith, L.D. Mech, and L.E. Eberly. 2009. Body size and predatory performance in wolves: is bigger better? *Journal of Animal Ecology* , **1** :532–539.

Massey, A.L., G.H. Roffler, T. Vermeul, J.M. Allen, and T. Levi. 2021. Comparison of mechanical sorting and DNA metabarcoding for diet analysis with fresh and degraded wolf scats. *Ecosphere* , **12** :03557.

Mattioli, L., C. Capitani, A. Gazzola, M. Scandura, and M. Apollonio. 2011. Prey selection and dietary response by wolves in a high-density multi-species ungulate community. *European Journal of Wildlife Research* , **57** :909-922.

Mech, D.L., T.J. Meier, J.W. Burch, and L.G. Adams. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. In Ecology and conservation of wolves in a changing world. Edited by L.N. Carbyn, S.H. Fritts, and D.R. Seip. Can. Circum. Inst. Occas. Publ. No. 35

Mech, L.D. 1966. *The Wolves of Isle Royale . Fauna of the National Parks of the United States Fauna Series* 7, *https://doi.org/10.1002/j.2326-1951.1967.tb00277.x*

Messier, F., and M. Crête. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia* , **65** :503-512.

Metz, C.M., Smith, D.W., Vucetich, J.A., Stahler, D.R., and Peterson, R.O. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* , **81** : 553-563.

Metz, M.C., D.W. Smith, J.A. Vucetich, D.R. Stahler, and R.O. Peterson. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* , **81** :553–563.

Mukherjee, S. and M.R. Heithaus. 2013. Dangerous prey and daring predators: a review. *Biological Reviews* , **88** :550–563.

Muller, S. 2006. Diet composition of wolves (*Canis lupus*) on the Scandinavian peninsula determined by scat analysis. English summary of the diploma thesis, School of Forest Science and Resource Management, Technical University of Munchen, Germany.

National Park Service. 2018. Isle Royale National Park. Environmental impact statement to address the presence of wolves.

Newsome, T.M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C.R., Dellinger, J.A., Lopez-Bao, J.V., Peterson, R.O., Shores, C.R., Wirsing, A.J. and Ripple, W.J. 2016. Food habits of the world's grey wolves.*Mammal Review* , **46** :255-269.

Orning, E.K., Dugger, K.M. and Clark, D.A. 2021. Gray wolf (*Canis lupus*) predation patterns following recent recolonization in a multi-predator, multi-prey system. *Canadian Journal of Zoology* , **99** (10):902-911.

Orning, E.K., M.C. Romanski, S. Moore, Y. Chenaux–Ibrahim, J. Hart, and J.L. Belant. 2020. Emigration and First-Year Movements of Initial Wolf Translocations to Isle Royale. *Northeastern Naturalist* , **27** :701–708.

Paquet, P.C. 1989. Behavioral ecology of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding National Park, Manitoba. PhD thesis, University of Alberta, Edmonton.

Parker, K.L. 2003. Advances in the nutritional ecology of cervids at different scales. *Ecoscience,* **10** :395–411

Petroelje, T.R., J.L. Belant, D.E. Beyer, G. Wang, and B.D. Leopold. 2014. Population-level response of coyotes to a pulsed resource event.*Population Ecology,* **56** :349–358.

Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* , **52** :137–154.

Ripple, W.J. and R.L Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation* , **145** :205–213.

Romanski, M.C. 2010. Estimates of abundance and predation–the population ecology of beaver in Isle Royale National Park (Doctoral dissertation, Michigan Technological University).

Rosell, F., O. Bozser, P. Collen, and H. Parker. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* , **35** :248-276.

Sanchez, D.M., P.R. Krausman, T.R. Livingston, and P.S. Gipson. 2004. Persistence of carnivore scat in the Sonoran Desert. *Wildlife Society Bulletin* , **32** :366-372.

Sand, H., J.A. Vucetich, B. Zimmermann, P. Wabakken, C. Wikenros, H.C. Pedersen, R.O. Peterson, and O. Liberg. 2012. Assessing the influence of prey-predator ratio, prey age structure and packs size on wolf kill rates. *Oikos* , **121** :1454–1463.

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

Sanders, S., and J. Grochowski. 2013. The forests of Isle Royale National Park: can we preserve this pristine wilderness in the face of climate change? *Natural Areas Journal* , **33** :66-77.

Severud, W.J., T.R. Obermoller, G.D. Delgiudice, and J.R. Fieberg. 2019. Survival and cause-specific mortality of moose calves in northeastern Minnesota. *The Journal of Wildlife Management* , **83** :1131–1142.

Smith, D.W., and R.O. Peterson. 2021. Intended and unintended consequences of wolf restoration to Yellowstone and Isle Royale National Parks. *Conservation Science and Practice* , **3** :413.

Spaulding, R., P.R. Krausman, and W.B. Ballard. 2000. Observer bias and analysis of gray wolf diets from scats. *Wildlife Society Bulletin,* **28** :947–950.

Stahler, D.R., D.W. Smith, and D.S. Guernsey. 2006. Foraging and feeding ecology of the gray wolf (Canis lupus): lessons from Yellowstone National Park, Wyoming, USA. *The Journal of Nutrition* , **136** :923S-1926S.

Stephens, P.W. and R.O. Peterson. 1984. Wolf-avoidance strategies of moose. *Ecography* , **7** : 239–244.

Suraci, J.P., M. Clinchy, L.M. Dill, D. Roberts, and L.Y. Zanette. 2016. Fear of large carnivores causes a trophic cascade. *Nature Communications* , **7** :1–7.

Svoboda, N.J., J.L. Belant, D.E. Beyer, J.F. Duquette, and J.A. Martin. 2013. Identifying bobcat Lynx rufus kill sites using a global positioning system. *Wildlife Biology* , **19** :78-86.

Tallian, A., D.W. Smith, D.R. Stahler, M.C. Metz, R.L. Wallen, C. Geremia, J. Ruprecht, C.T. Wyman, and D.R. MacNulty. 2017. Predator foraging response to a resurgent dangerous prey. *Functional Ecology* , **31** :1418-1429.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G., Orihuela, M. Riveros, R. Ascanio, G.H. Adler, T.D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* , **294** :1923-1926.

Theuerkauf, J. 2009. What drives wolves: fear or hunger? Humans, diet, climate and wolf activity patterns. *Ethology* , **115** :649-657.

Thurber, J.M., and R.O. Peterson. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. *Journal of Mammalogy* , **74** :879–889.

Tischler, K.B., W.J. Severud, R.O. Peterson, and J.K. Bump. 2019. Aquatic macrophytes are seasonally important dietary resources for moose. *Diversity* , **11** :209.

Vucetich, J.A., Vucetich, L.M. and Peterson, R.O. 2012. The causes and consequences of partial prey consumption by wolves preying on moose. *Behavioral Ecology and Sociobiology* , **66** (2):295-303.

Wam, H.K., and O. Hjeljord. 2003. Wolf predation on moose-a case study using hunter observations. *Alces* , **39** :263-272.

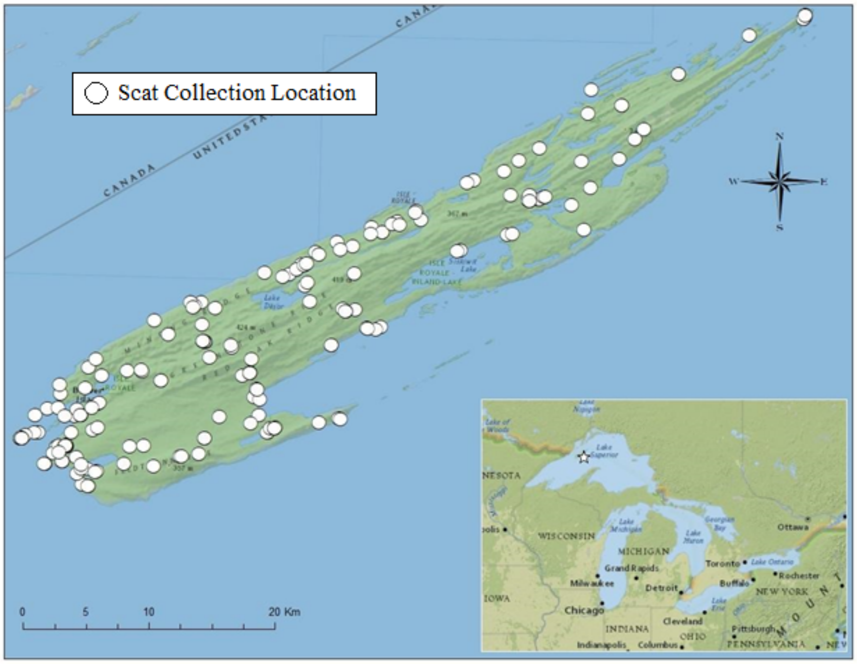


Figure 1. Locations of wolf scats collected (white circles) used to determine diet composition, Isle Royale National Park, Michigan, USA, May–October 2019 and June–September 2020.

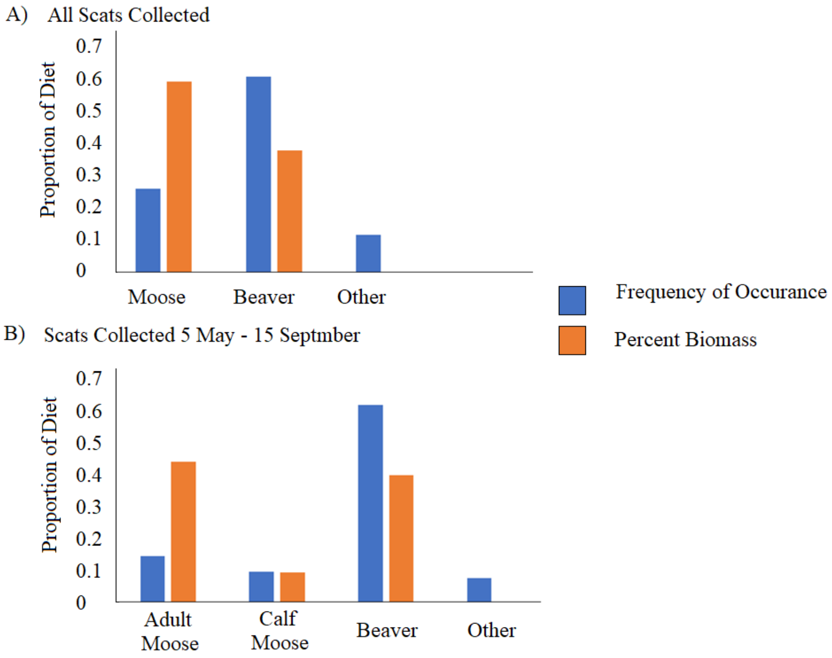
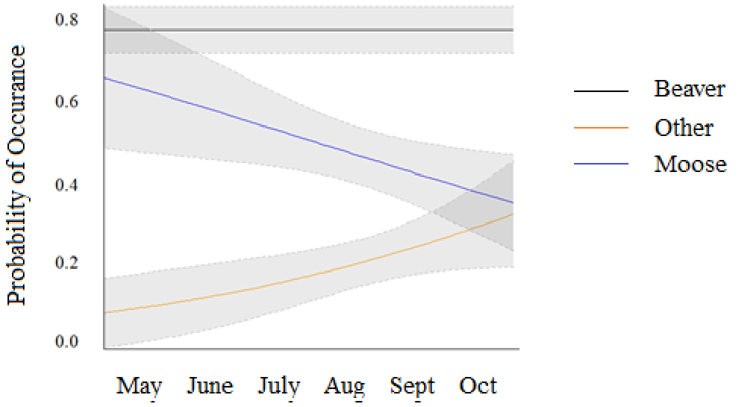


Figure 2. Proportional composition of prey identified in wolf scats, Isle Royale National Park, Michigan, USA by percent frequency of occurrence (blue bar), and percent biomass (orange bar). A) Scats collected with moose adults and calves pooled. B) Scats collected with adult moose and calves separated.


A) All Scats Collected

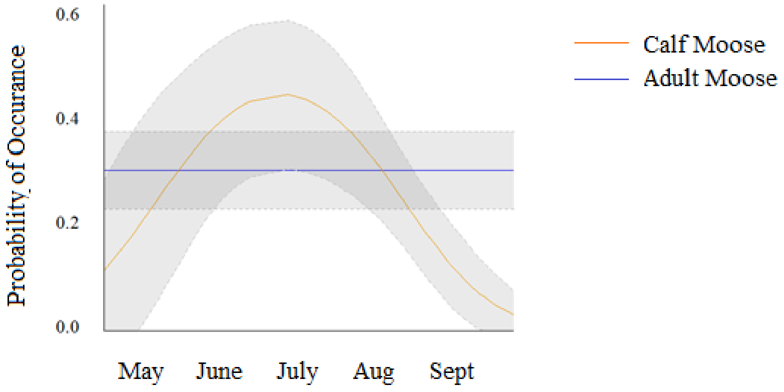

B) Scats Collected 5 May - 15 September

Figure 3. Temporal change in prey occurrence from wolf scats collected on Isle Royale National Park, Michigan, USA. A) Scats collected with moose adults and calves pooled. B) Scats collected with adult moose and calves separated.

Table 1. Occurrence of prey items (hair) identified from 206 wolf (*Canis lupus*) scats collected 5 May–22 October 2019 and 13 June–22 September 2020, Isle Royale National Park, Michigan, USA.

Prey Item	Number of points	Number of scats
Beaver	3119	161
Moose		
Moose Calf[1]	446	42
Moose Adult[1]	697	55
Moose[2]	187	15
Other		
Bird	93	8
Snowshoe Hare	118	9
Unknown	444	10
Wolf	85	10
Total	5042	206

[1] Age class identified for scats collected between 5 May–15 September

[2] Hair identified from scats collected after 15 September or when age could not be identified

Table 2. Logistic regression model selection results for moose (adults and calves pooled), beaver, and other prey occurrence in wolf scats collected 5 May–22 October 2019 and 13 June–22 September 2020, Isle Royale National Park, Michigan, USA.

	Model	K*	AICc*	ΔAICc*	${}_{i}$*	LL*
Moose	Linear	2	281.29	0	0.69	–138.62
	Nonlinear	3	283.13	1.84	0.27	–138.5
	Constant	1	287.11	5.82	0.04	–142.55
Beaver	Constant	1	217.30	0	0.44	–107.64
	Linear	2	217.83	0.53	0.34	–106.89
	Nonlinear	3	218.76	1.46	0.21	–106.32
Other	Linear	2	211.74	0	0.47	–103.84
	Nonlinear	3	211.79	0.05	0.46	–102.84
	Constant	1	215.71	3.97	0.06	–106.85

*K= number of parameters in model, AICc = Akaike Information Criterion corrected for small sample size, ΔAICc= difference between the AICc value of each model and the lowest AICc model, ${}_{i=}$ AICc weight, LL= negative log likelihood.

Table 3. Logistic regression model selection results for adult and calf in wolf scats collected 5 May–15 September 2019 and 13 June–15 September 2020, Isle Royale National Park, Michigan, USA.

	Model	K*	AICc*	ΔAICc*	${}_{i}$*	LL*
Adult	Constant	1	192.95	0	0.66	–95.46
	Linear	2	195	2.05	0.24	–95.46
	Nonlinear	3	196.73	3.78	0.1	–95.29
Calf	Nonlinear	3	163.28	0	0.98	–78.56
	Linear	2	171.83	8.55	0.01	–83.87
	Constant	1	175.24	11.97	0	–86.61

*K= number of parameters in model, AICc = Akaike Information Criterion corrected for small sample size, ΔAICc= difference between the AICc value of each model and the lowest AICc model, ${}_{i=}$ AICc weight, LL= negative log likelihood.