

Population-level response of coyotes to a pulsed resource event

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Abstract From foraging theory, generalist predators should increase consumption of prey if prey availability increases. Pulsed resource events introduce a large influx of prey to predators that may exhibit a functional response of increased consumption rate on, or specialization to, this abundant food resource. We predicted that coyotes (*Canis latrans*) would respond functionally to numerical increases of neonate white-tailed deer (*Odocoileus virginianus*) during the pulsed resource event of parturition. We used howl surveys and deer camera surveys with occupancy modeling to estimate densities for coyotes, adult deer, and fawns, respectively, in Upper Peninsula of Michigan, USA, 2009–2011. We estimated biomass of adult and fawn deer consumed by coyotes during 2 periods [fawn limited mobility period (LMP) and social mobility period (SMP)] in May–August each year. Coyote densities were 0.32 and 0.37/km² for 2010–2011, respectively. Adult deer densities (3.7–3.9/km²) and fawn densities (0.6–1.3/km²) were similar across years. Overall, fawn hair occurrence in coyote scats was 2.3 times greater in LMP than SMP. Estimated consumption of fawns between periods ($n = 157$ –880) by coyotes varied, suggesting a functional

response, with increasing consumption of fawns relative to their availability. Coyotes, on average, consumed 2.2 times greater biomass of fawns than adults across years, and consumed 1.5 times greater fawn biomass, on average, during LMP than SMP. We suggest that consumption rates of coyotes is associated positively with increases in fawn density, and fawn consumption by coyotes follows predictions of optimal foraging theory during this pulsed resource event.

Keywords *Canis latrans* · Consumption · Foraging theory · Functional response · *Odocoileus virginianus*

Introduction

Foraging theory seeks to explain patterns of food selection by animals, including predators (Krebs 1978). Changes in prey abundance can influence food acquisition rates and subsequently fitness of predators, resulting in numerical responses of their populations. For example, lynx (*Lynx canadensis*), a specialist of snowshoe hare (*Lepus americanus*), increase in abundance in response to increases in hare abundance (O’Donoghue et al. 1997). However, foraging theory also predicts that an opportunistic predator will exhibit a functional response and increase prey consumption as prey availability increases, until satiated (Holling 1959; Krebs 1978). Thus, for generalist predators we would expect greatest predation of prey to occur when prey availability is greatest.

Pulsed resource events are brief, large magnitude influxes of food that occur infrequently [e.g., acorn mast (Yang et al. 2008)]. Pulsed resource events can influence generalist predator foraging behavior through increased consumption of readily available prey (Yang et al. 2008).

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Use of pulsed resources by predators varies across species, and can be influenced by abundance of the food resource, availability of alternative prey, and prey size relative to the predator (Careau et al. 2008; Yang et al. 2008). Predators have exhibited functional responses to pulsed resource events, for example Arctic fox (*Alopex lagopus*) increased consumption of greater snow goose (*Chen caerulescens atlanticus*) eggs, a pulsed resource, when lemming (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*) abundance was low (Careau et al. 2008).

A positive association exists between predator body mass and body mass of their prey (Griffiths 1980; Carbone et al. 1999; Brose et al. 2008). For example, species within Carnivora weighing <21.5 kg are more likely to consume prey $\leq 45\%$ of their body mass (Carbone et al. 1999). Within social predators, larger groups take larger prey compared to smaller groups or individuals of that species, as seen in African wild dogs [*Lycaon pictus* (Creel and Creel 1995)] and gray wolves [*Canis lupus* (Schmidt and Mech 1997)]. In contrast, solitary predators tend to take prey of sizes proportional to their body mass, for example leopards (*Panthera pardus*), a solitary predator, selected smaller prey than dhole (*Cuon alpinus*) a group-hunting predator, even though adult body mass of leopards is greater than adult body mass of dholes (Karanth and Sunquist 1995). Thus, if a prey source becomes readily available, it is likely a generalist predator will increase consumption of that prey if it is within the optimal prey size for the predator.

Coyotes (*Canis latrans*, Say, 1823) are a small (median body mass = 12.0 kg, 13 studies; Bekoff and Gese 2003) predator and typically solitary hunter during summer (Gese et al. 1988). Coyotes consume a diverse diet including insects, vegetation, fish, birds, small mammals, ungulate neonates, and lagomorphs (Bekoff 1977; Rose and Polis 1998), and are considered generalists that consume energetically advantageous prey that are most available (Gese et al. 1988; Boutin and Cluff 1989). Predicted optimal prey size of coyotes is $\leq 45\%$ (<6.0 kg) of their body mass (Carbone et al. 1999). Although prey larger than coyotes (e.g., adult white-tailed deer, *Odocoileus virginianus*, Zimmerman, 1780) may be available and coyotes can more easily kill large prey when hunting in groups (Ozoga and Harger 1966; Gese et al. 1988; Brundige 1993), prey exceeding 6 kg may not be energetically advantageous for solitary coyotes to capture, and may come at greater risk (Carbone et al. 1999). Thus, predation by coyotes on white-tailed deer fawns following parturition would likely be greater than predation on adults, as neonate fawns are within the predicted optimal prey size range of coyotes likely due to greater vulnerability (Nelson and Woolf 1987), smaller body size, and abundance of fawns following parturition. As coyotes would experience less risk and expend

less energy killing a fawn compared to an adult deer, we may consider fawns and adults separate prey sources.

Coyote predation can comprise up to 80 % of fawn white-tailed deer mortality within 1–3 months post fawn parturition (Whittaker and Lindzey 1999; Grovenburg et al. 2011). Combined with other mortality agents (e.g., starvation, vehicle collisions), coyotes can decrease survival of white-tailed deer fawns to 34 % after 1 month and 13 % by 3 months post parturition, respectively (Whittaker and Lindzey 1999; Grovenburg et al. 2011). In contrast, predation on adult deer by coyotes during summer is low, representing 20–30 % of the coyote's diet (Patterson et al. 1998). As coyotes are opportunistic, predation on fawns would likely be greatest soon after peak resource availability [i.e., parturition (McGinnes and Downing 1977; Verme et al. 1987)] and during years when number of fawns born are greatest. Following peak parturition, fawn availability would decline as mortality events occur, and at lesser prey densities energetic costs of hunting fawns would increase as coyotes expended more time searching (Krebs 1978). Also, fawn mobility increases 35 days post-parturition (Ozoga et al. 1982) and antipredator behavior of fawns switches from hiding to running (Nelson and Woolf 1987), which would further increase energetic costs of predation by coyotes. Finally, based on growth rates of fawns (Verme and Ullrey 1984) and predicted optimal prey size of coyotes (Carbone et al. 1999), fawns would exceed predicted optimal prey size of coyotes 20–35 days post-parturition. Changes in fawn availability and vulnerability as body size increases would likely decrease their use by coyotes.

We examined consumption response of a generalist predator to a pulsed resource event. Specifically, we estimated population-level consumption rates of fawn and adult white-tailed deer by coyotes and compared consumption rates across years. We hypothesized that coyotes would respond functionally to white-tailed deer parturition, with coyote consumption of fawns increasing immediately following parturition and during years of greater fawn abundance. We predicted greatest consumption of fawns by coyotes would be near peak parturition. We further predicted consumption of fawns would decline as fawns decreased in abundance and increased in mobility and body mass. In addition, because optimal prey size of coyotes is predicted to be ≤ 6 kg, we predicted coyotes would consume fewer and relatively constant numbers of adult deer.

Methods

Study area

The study area included about 850 km² in Delta and Menominee counties in Michigan's Upper Peninsula

(45.6°N, 87.4°E; Fig. 1) and is characterized by limestone bedrock, ground moraine, cedar swamps, northern hardwood forest, and coastal marshes (Albert 1995). Land ownership consists of private and public lands including the Escanaba River State Forest. Predominant land covers include 52 % woody wetlands [e.g., black spruce (*Picea mariana*), green ash (*Fraxinus pennsylvanica*), northern white cedar (*Thuja occidentalis*), speckled alder (*Alnus incana*)], 14 % deciduous forest (e.g., sugar maple [*Acer saccharum*], quaking aspen [*Populus tremuloides*]), and 14 % agriculture (i.e., row crops and pastures). The remaining 20 % includes conifer forest, mixed forest, developed areas, herbaceous wetlands, shrub, and open water (2006 National Land Cover Data, Fry et al. 2011). Elevations range from 177 to 296 m. The western portion of the study area contains more agriculture and a rolling landscape. Average monthly high and low temperatures during May–September 2009–2011 were 24.3 °C during July and 3.3 °C during May, respectively. Average rainfall was 22.3 cm during May–September 2009–2011

[Escanaba, MI airport Automated Surface Observation System (National Weather Service 2011)].

Coyote howl surveys

We divided the study area into 4 survey sections with 55 non-overlapping survey points (Fig. 1). We established a 2 km buffer around each survey point representing the farthest consistent distance of coyote audibility to humans (Fuller and Sampson 1988; Petroelje et al. 2013). The 55 survey points including 2 km buffers comprised 690.8 km² (81 %) of the study area. We conducted howl surveys from dusk until 0300 h, August–September 2009 and July–September 2010–2011. Each month we conducted a howl survey using a coyote group-yip call during the first week, followed by a howl survey using a lone wolf call during week 2. We used both call types for density estimates as Petroelje et al. (2013) found coyote vocalization response rates to coyote group-yip howls and lone wolf howls to be similar. We did not conduct howl surveys during weeks

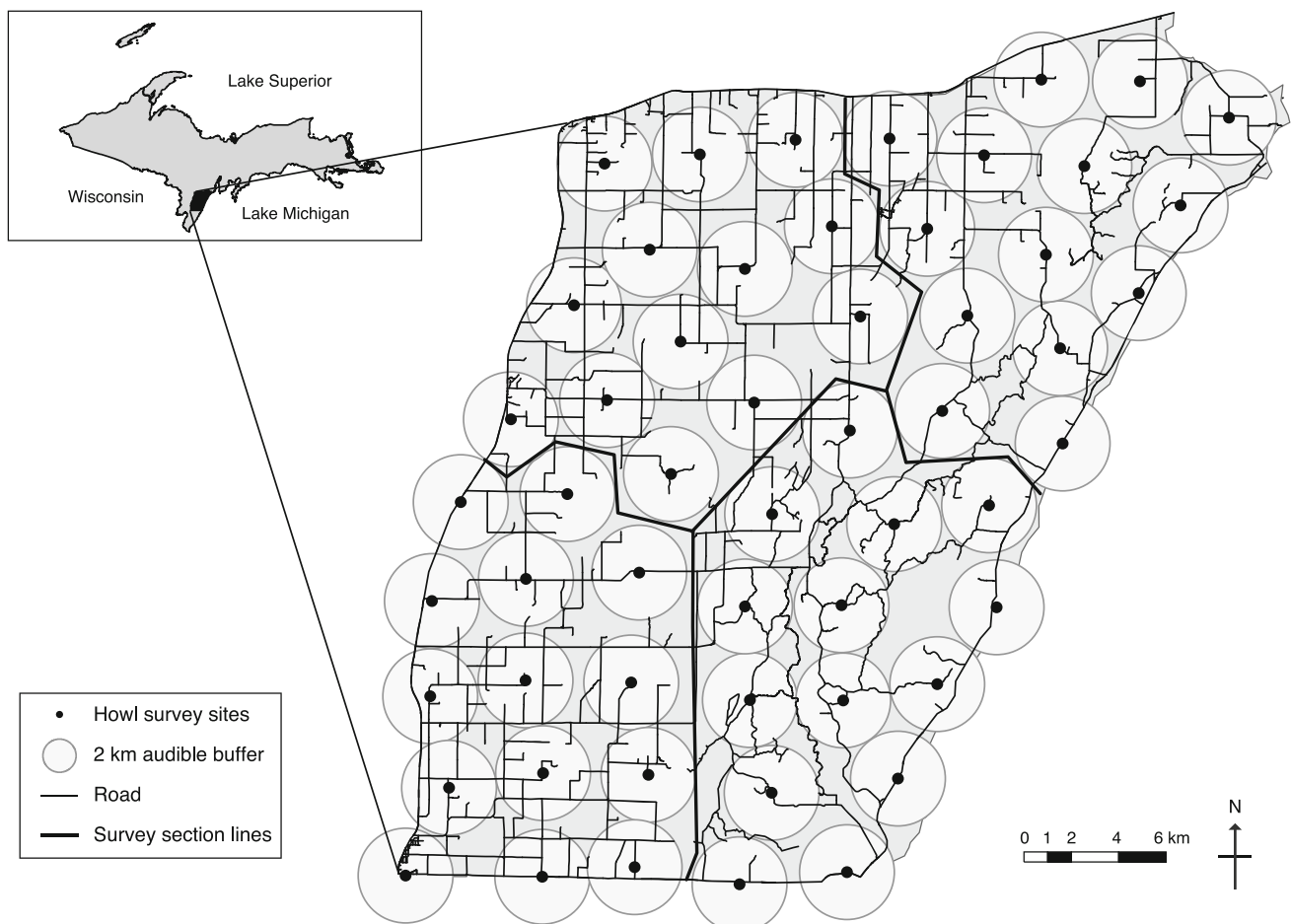


Fig. 1 Locations of 55 howl survey sites with 2 km buffers for detecting coyote vocal responses in 4 survey sections, Upper Peninsula of Michigan, 2009–2011

3–4 to limit potential habituation to broadcasted calls (Wenger and Cringan 1978). We attempted to visit all survey points in each survey section in one night such that we completed each howl survey in 4 consecutive nights, weather permitting. We elicited coyote vocalizations using a FX3 game caller (FoxPro, Lewiston, Pennsylvania, USA) with a group-yip howl (Lehner 1982) or a lone wolf howl, alternating between flat and breaking howls (Harrington and Mech 1982). During all observed responses, we aurally estimated number of individuals responding within a pack. We stopped surveys when wind speed exceeded 12 km/h (Kestrel 1000, Nielsen-Kellerman Inc., Boothwyn, Pennsylvania, USA) or precipitation occurred as these conditions may limit responses (Harrington and Mech 1982), and continued surveys the next suitable night.

Coyote abundance estimates

We estimated coyote density using function `occuRN` within package `unmarked` (Fiske and Chandler 2011) for R 2.14.2 software (R Development Core Team 2011). Using the abundance mixture model of Royle and Nichols (2003) we modeled abundance of each site (N_i) fit to a Poisson distribution. We modeled detection of an individual (r) as a Bernoulli trial at each sample unit to estimate detection probability (p_i) over time. In this way, we related heterogeneity in N_i to heterogeneity in p_i following Royle and Nichols (2003) where:

$$p_i = 1 - (1 - r)^{N_i}$$

In this case, we used p_i when constructing likelihood of detection while accounting for heterogeneity across the landscape (see Royle and Nichols 2003).

We estimated coyote density using vocal responses as binary data (presence or absence) and occupancy modeling that accounted for heterogeneity in detection (Royle and Nichols 2003). At least one individual responding to the broadcasted call represented detection of individuals at each survey point. We included a time dependent variable to observe if detection changed during survey months (July–September) and a habitat variable [i.e., percent forest cover (upland and lowland coniferous and deciduous forests combined) and agriculture; Fry et al. 2011] to discern if abundance varied between habitats. We used a global model to describe variation in detection (time) and abundance (habitat), a null model assuming constant detection and abundance, and 2 remaining models assuming either detection or abundance varied while the other remained constant.

We ranked and weighted models using Akaike Information Criterion adjusted for small sample size (AIC_c) to select the most parsimonious model(s) for each year (Burnham and Anderson 2002). We considered models

with lesser AIC_c scores as better models; however, we also used Akaike weights for model selection uncertainty (Burnham and Anderson 2002). Inference from model averaging is not known across models that include variables of occupancy (Royle and Nichols 2003), therefore we used density estimates from top-ranking models only to extrapolate to non-surveyed portions of the study area.

Deer abundance estimates

We used estimates of adult and fawn white-tailed deer abundance and density obtained within 249 km² of the central portion of our study area (J.F. Duquette et al., unpublished data) and assumed this was representative of our study area. Fifty-five remote cameras were used in surveys conducted during September–October 2009–2011 and occupancy models of Royle and Nichols (2003) for unmarked individuals to estimate deer density. The null model assuming constant detection across time and constant abundance across space performed best (J.F. Duquette et al., unpublished data). Thus, we did not use any landscape variable to account for variation across our study area. Adult female and male relative abundance were similar across years, but fawn relative abundance was greater in 2010 than in 2009 and 2011. Combined adult female and male deer density in 2009 was 3.9/km² (SE = 1.49), 3.7/km² (SE = 1.37) in 2010, and 3.3/km² (SE = 0.48) in 2011. Fawn density in 2009 was 0.6/km² (SE = 0.25), 1.3/km² (SE = 0.50) in 2010, and 0.8/km² (SE = 0.19) in 2011.

Scat collection and analysis

We collected coyote scats opportunistically from May to August 2009–2011 and only included scats found ≥ 2 days after the earliest estimated date of fawn parturition each year in our analysis. We considered scats with adjacent coyote tracks as coyote scats (Prugh and Ritland 2005). For scats not associated with tracks we used the criterion of Thompson (1952) and Green and Flinders (1981) to differentiate among coyotes, gray wolves, and red fox (*Vulpes vulpes*), where scats >18 mm and <25 mm diameter with tapered ends were classified as coyote (see also Mech 1970; Peterson 1974; Van Ballenberghe et al. 1975). We placed coyote scats in plastic bags and labeled each sample with location, date, and if coyote tracks were present.

We washed scats in nylon bags so that only hair, bone fragments, and hooves remained, and then dried these contents (Johnson and Hansen 1979). We identified deer hair as adult or fawn using microscopic scale patterns, coloration, and length (Adorjan and Kolenosky 1969). One lab technician analyzed scats to reduce observer error in identification of prey remains. We identified percent

volume of each coyote scat that contained adult or fawn deer hair during each period (described below) of 2009–2011 to estimate deer biomass consumed. We used estimated parturition dates of captured fawns (Duquette et al. 2011) to compare to dates of fawn hair appearing in scat to observe how quickly coyotes responded to deer parturition. We assumed percentage volume of coyote scats with adult or fawn deer hair represented presence of adult or fawn deer in the coyote diet as a caloric intake during 24 May–31 August 2009–2011.

Fawns exhibit limited mobility until 35 days post-parturition at which time they become socially mobile and move with family groups (Ozoga et al. 1982). Thus, we summarized proportions of coyote scats containing fawn and adult hair during the limited mobility period (LMP, 24 May–30 June) and social mobility period (SMP, 1 July–31 August) until fawns attained adult pelage (about 1 September; Sauer 1984). During LMP fawn behavior is characterized by bedding with little movement to avoid predation, whereas during SMP fawns join social groups and run to avoid predation (Ozoga et al. 1982).

Estimating number of deer consumed

We used the estimated daily basal metabolic rate ($94.47 \text{ kcal} \times \text{kg}^{0.75}$; Litvaitis and Mautz 1980) and estimated daily minimum energy requirements for free-ranging coyotes ($\sim 2.0\text{--}2.5 \times$ basal metabolic rate; Laundré and Hernández 2003) to calculate daily field metabolic rate. Laundré and Hernández (2003) found no difference in energetic requirements for un-mated males and females whereas male and female mated individuals had annual increased caloric requirements compared to un-mated individuals. We assumed a 50:50 coyote sex ratio, with 53 % of the population being adult (average value from Knowlton 1972; Gese et al. 1989). We assumed 54 % of the adult female population had dependent young (Knowlton 1972) during LMP and mated individuals (male and female) had to supply pups with 540.7 kcal/day during this time (Laundré and Hernández 2003). During SMP we assumed pups were no longer dependent on mated individuals to provide resources (Laundré and Hernández 2003). Thus, we calculated energy requirements for 54 and 46 % of the adult coyote population using mated ($186.2 \text{ kcal/kg}^{0.75}$, male and $189.1 \text{ kcal/kg}^{0.75}$, female) and un-mated ($185.6 \text{ kcal/kg}^{0.75}$ day) daily caloric requirements, respectively.

To estimate mean coyote body mass used in our calculations of energetic requirements, we captured coyotes during May–July 2009–2011 using #3 padded foot-hold traps (Oneida Victor, Cleveland, Ohio, USA) and during March 2011 using cable neck restraints (Etter and Belant 2011). We anesthetized coyotes with a ketamine

hydrochloride (4 mg/kg; Ketathesia, Bioniche Teoranta Inverin, Co., Galway, Ireland) and xylazine hydrochloride (2 mg/kg; IVX Animal Health, Inc., St. Joseph, MO, USA) mixture (Kreeger and Arnemo 2007). We recorded gender, morphometrics, applied ear tags, and weighed each individual. We administered yohimbine hydrochloride (0.15 mg/kg; Yobine, Ben Venue Laboratories, Benford, Ohio, USA) as a reversal for xylazine (Kreeger and Arnemo 2007) before we released coyotes at their respective capture sites. We received approval for all capturing and handling procedures through Mississippi State University's Institutional Animal Care and Use Committee (protocol 09-004).

We used mean coyote body mass to estimate daily field metabolic rate with Laundré and Hernández (2003) equation for both breeding and non-breeding proportions of the population to estimate the energetic requirements of the coyote population during LMP and SMP 2010–2011. Proportion of coyote diet consisting of adult or fawn deer was multiplied by total energetic requirement (in kcal) to estimate the caloric demand fulfilled from adult or fawn deer during LMP and SMP.

We used Litvaitis and Mautz's (1980) estimates of 1,657.9 kcal/kg for the caloric value of white-tailed deer meat (28.1 % of the gross caloric value of dry matter; 5,900 kcal/kg) and 84.6 % (1,402.6 kcal/kg) as the metabolized energy of deer by coyotes to estimate caloric values provided by a diet of adult or fawn deer during each period. We used deer captured during 2009–2011 to estimate mean body mass of adults (≥ 1.5 years old, $n = 101$, $\bar{x} = 66.3 \text{ kg}$, $\text{SD} = 13.9$) and date of parturition as well as body mass of fawns (Table 1) during both periods (Duquette et al. 2011). As fawns age, their body masses increase resulting in a change in total kcal available to coyotes. Therefore, we used median date of presence of fawn hair in scat for each period and estimated fawn weight at that time following Verme and Ullrey's (1984) estimate of fawn weight gain (0.2 kg/day) to estimate median fawn weight during LMP and SMP.

Table 1 Mean white-tailed deer fawn weights at birth, median parturition date (Duquette et al. 2011), and estimated median weights of neonates during fawn limited mobility period (LMP, 24 May–30 June) and social mobility period (SMP, 01 July–31 August) using date of hair in scat, Upper Peninsula of Michigan, 2009–2011

Year	\bar{x} Birth mass (SD)	Median date of parturition	Median LMP body mass	Median SMP body mass
2009	2.37 (0.82)	02 Jun (50)	4.2 (34)	12.6 (6)
2010	4.19 (1.57)	02 Jun (44)	6.0 (41)	13.8 (6)
2011	4.10 (0.91)	01 Jun (49)	5.3 (26)	15.1 (9)

All mass values in kg; sample sizes in parentheses unless otherwise stated

We calculated biomass and number of adult and fawn deer consumed during LMP and SMP in 2010–2011 following Patterson et al. (1998), but estimated proportion of diet that was adult or fawn deer, and calculated total number of prey consumed for the population of coyotes rather than an individual:

$$B_x = \frac{T_x n(C_x \alpha_x)}{K_x}$$

where B_x represents biomass of adult (B_A) or fawn (B_F) deer consumed, T_x is number of days in each period ($T_{LMP} = 38$; $T_{SMP} = 62$), n is abundance estimate of coyotes, C_x is daily caloric requirements for breeding (C_B) or non-breeding (C_N) proportions of the coyote population, α_x is proportion of scat volume containing adult (α_A) or fawn (α_F) hair, and K_x is metabolized energy provided by an adult or fawn deer (1,402.6 kcal). To estimate the number of adult or fawn deer consumed during each period each year we divided biomass estimates by the estimated weight of an adult (66.3 kg) or fawn during LMP (2010, 6.0 kg; 2011, 5.9 kg) or SMP (2010, 13.8 kg; 2011, 14.7 kg).

Results

Coyote howl surveys

We observed an overall 24 % coyote response rate and elicited responses at 34, 43, and 43 sites during 2009–2011, respectively. From aural responses, we estimated a mean of 46 and 56 coyotes responding during 2010 and 2011 surveys, respectively. We were unable to estimate coyote abundance for 2009 because too few surveys were conducted; however, mean number of aurally estimated coyotes responding ($n = 53.5$) was similar to 2010–2011 averages.

The most parsimonious coyote abundance model for 2010 and 2011 included constant abundance and detection (Table 2). We excluded a competing model for 2010 which included constant detection and varying abundance with an inverse relationship between percentage forest cover and coyote abundance. Estimates of coyote detection were 7.5 % (SE = 4.7) in 2010 and 6.2 % (SE = 4.2) in 2011, respectively. Estimated coyote density during 2010 and 2011 was 0.37/km² [95 % CI (0.21, 0.54)] and 0.32/km² [95 % CI (0.17, 0.47)], respectively. Abundance estimates for the entire study area were 314 [95 % CI (179, 459)] coyotes in 2010 and 272 [95 % CI (145, 400)] coyotes in 2011.

Scat analysis

We analyzed 149, 139, and 76 coyote scats for presence of fawn and adult deer hair during 2009–2011, respectively.

Table 2 Model selection using Akaike Information Criterion adjusted for small samples (AIC_c) for factors influencing coyote vocal response to estimate abundance, Upper Peninsula of Michigan, June–September 2010–2011

Year	Model ^a	Model parameters	AIC _c	ΔAIC _c ^b	wt ^c
2010	~int ~int	2	366.7	0	0.64
	~int	4	367.9	1.22	0.34
	~forest + agri				
	~date ~int	3	373.4	6.73	0.02
	~date	5	374.7	7.97	0.01
2011	~int ~int	2	379.5	0	0.92
	~int	4	384.9	5.47	0.06
	~forest + agri				
	~date ~int	3	386.8	7.33	0.02
	~date	5	392.3	12.82	<0.01
	~forest + agri				

^a Model parameters included habitat (forest = percent of each site that was forested, agri = percent of each site that was agriculture) as a covariate of abundance and time of each survey (date = day survey was conducted) as a covariate of detection. The intercept was also estimated (int = intercept)

^b Difference between first model and selected model AIC_c scores

^c Akaike weight; proportion of support for each model

Overall, volume of fawn hair in coyote scat declined markedly from LMP ($\bar{x} = 52$ %) to SMP ($\bar{x} = 22$ %). Volume of fawn hair in coyote scat during LMP increased from 34 to 43 % and finally 79 % during 2009–2011, respectively (Fig. 2). In contrast, volume of fawn hair in scat during SMP varied only 7 % (19–26 %) across years. Volume of adult deer hair in coyote scat was always less than fawn hair, except during SMP 2009 where volume of adult and fawn deer hair was similar (Table 3). Cumulative percentages of scats containing fawn hair followed trends in cumulative percentages of fawn births (Fig. 3) where coyotes appeared to start consuming fawns soon after they became available.

Estimating minimal energy requirements and number of deer consumed

Mean coyote body mass was 13.9 kg (SD = 1.1 kg, $n = 12$) and 11.3 kg (SD = 1.5 kg, $n = 13$) for males and females, respectively. We calculated daily field metabolic rate as 1,881.1 kcal ($186.2 \text{ kcal} \times 13.9 \text{ kg}^{0.75} + 540.7 \text{ kcal}$), 1,706.2 kcal ($189.1 \text{ kcal} \times 11.3 \text{ kg}^{0.75} + 540.7 \text{ kcal}$) for male and female breeding individuals during LMP, respectively. During SMP we calculated daily field metabolic rate as 1,340.4 kcal ($186.2 \text{ kcal} \times 13.9 \text{ kg}^{0.75}$), 1,165.5 kcal ($189.1 \text{ kcal} \times 11.3 \text{ kg}^{0.75}$) for male and female mated individuals, respectively. We calculated

Fig. 2 Percentage of coyote scats with white-tailed deer fawn hair during fawn limited mobility period (LMP, 24 May–30 June) and social mobility period (SMP, 01 July–31 August), Upper Peninsula of Michigan, 2009–2011

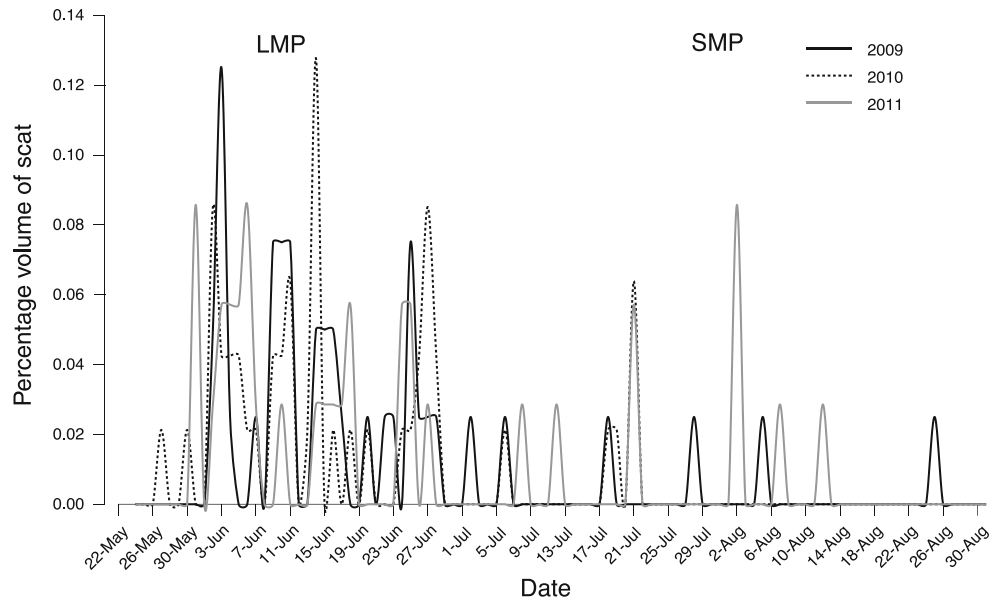


Table 3 Percent volume of coyote scats containing white-tailed deer hair during fawn limited mobility period (LMP, 24 May–30 June) and social mobility period (SMP, 01 July–31 August), Upper Peninsula of Michigan, 2009–2011

Deer age class	Time period	Percent volume of scats		
		2009	2010	2011
Fawn	LMP	34	43	79
	SMP	19	26	21
Adult	LMP	22	23	9
	SMP	21	13	14

unmated individuals daily field metabolic rate as 1,256.0 kcal ($185.6 \text{ kcal} \times 12.8 \text{ kg}^{0.75}$) for both LMP and SMP. Estimated body mass of fawns at birth were almost two times greater in 2010–2011 than in 2009 (Table 1).

Proportion of total energetic requirement provided by adult and fawn deer in coyote diet was 66 % in 2010 and 88 % in 2011 during LMP, and 39 % in 2010 and 35 % in 2011 during SMP. Adult deer comprised a relatively lesser percentage of coyote energetic requirements compared to fawns in 2010 and 2011 (Fig. 4a). During LMP, fawns met 43 and 79 % of coyote energetic requirements during 2010 and 2011, respectively. During SMP, fawns met 26 and 21 % of coyote energetic requirements during 2010 and 2011, respectively. Percentage of coyote energetic requirements provided by adult deer during LMP was 23 and 9 % in 2010 and 2011, respectively, and during SMP was 13 and 14 % in 2010 and 2011, respectively.

Total biomass of deer consumed was similar during 2010–2011 when coyote densities and deer densities were similar. Also, estimated numbers and biomass of fawns consumed did not differ between 2010 and 2011. Fawn

biomass consumed by coyotes was 1.9 times greater than consumption of adult biomass in 2010 and 3.5 times greater in 2011 (Fig. 4b). Coyotes consumed 2 times greater fawn biomass during LMP than SMP in 2011 but similar fawn biomass during these periods in 2010. Coyotes consumed 335 (62 %) more fawns during LMP 2011 than in LMP 2010. Coyotes consumed 2.3 times more fawns in LMP than SMP during 2010 and 5.6 times more fawns during 2011 (Fig. 4c). Coyotes consumed 16.4 and 74.4 times more fawns than adult deer during LMP in 2010 and 2011, respectively. In contrast, coyotes consumed 8.3–5.3 times more fawns than adult deer during SMP in 2010 and 2011, respectively.

Discussion

We observed a direct response of increased coyote consumption of neonate white-tailed deer to the pulsed resource of fawn parturition. Increased consumption of available pulsed resources has been observed in other carnivores including black bears [*Ursus americanus* (Reimchen 2000)], gray wolves [*Canis lupus* (Darimont and Reimchen 2002)], and arctic foxes [*Alopex lagopus* (Carcrau et al. 2008)]. Coyotes exploited fawns following parturition as expected by a generalist predator (Yang et al. 2008) possibly due to fawns being the most profitable resource available. Previous radio-telemetry studies of white-tailed deer fawn survival have demonstrated greatest mortality of fawns soon after parturition (Whittaker and Lindzey 1999; Grovenburg et al. 2011) as we observed occur in coyote response to fawn parturition (Fig. 3). Patterson et al. (1998) noted prey switching from snowshoe hare to fawns with onset of white-tailed deer parturition,

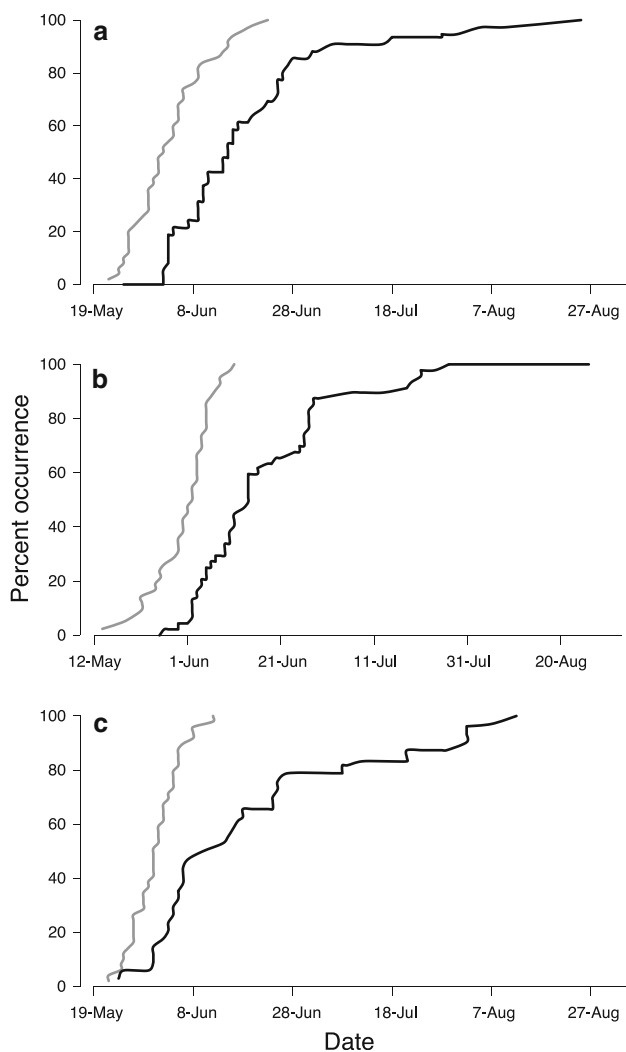


Fig. 3 Comparison of cumulative percent occurrence of captured white-tailed deer fawns born [grey line (Duquette et al. 2011)] and cumulative percent occurrence of coyote scats with fawn hair by date (black line) for 2009 (a), 2010 (b), and 2011 (c)

and similar to our findings, coyotes decreased use of the pulsed resource over time.

Although across year density estimates of coyotes were similar and fall fawn density and occurrence of fawn hair in scat varied more than two-fold, we were not able to detect if coyotes exhibited a functional response in fawn consumption between years. Although percent volume of scats may not detect changes in consumption as well as biomass models, it is more refined than percent occurrence of scats when a direct biomass model is not available (Klare et al. 2011). Previously, the proportion of a coyote's diet comprised of a particular prey was associated positively with density of that prey (O'Donoghue et al. 1998). In 2009 when fawn density was estimated at $0.6/\text{km}^2$, <50 % of 2010 and 75 % of 2011 estimates, proportion of fawn hair found in scat was also less. However, we observed a

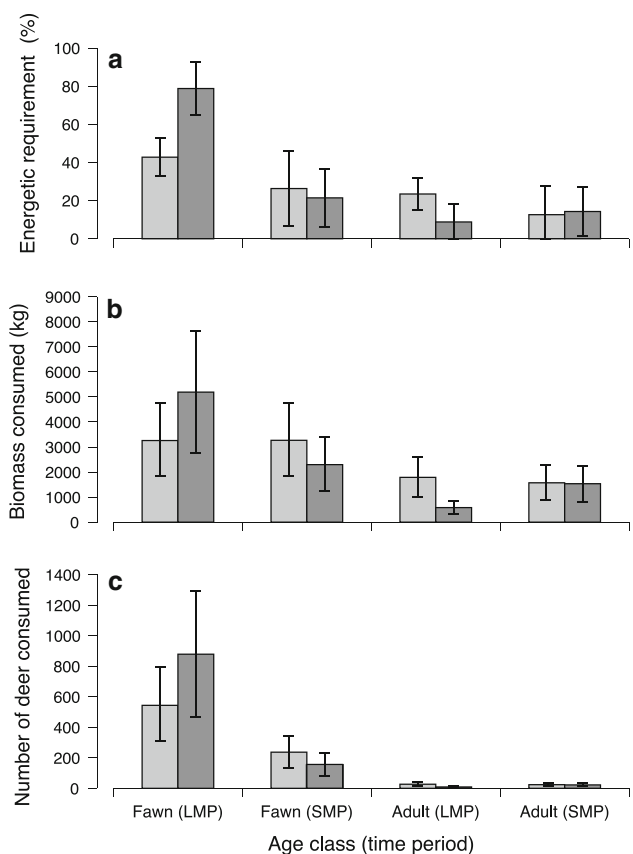


Fig. 4 a Estimated percentage of coyote energetic requirement acquired from white-tailed deer, b estimated biomass of deer consumed by coyotes, and c estimated number of deer consumed by coyotes (± 95 % confidence intervals) during fawn limited mobility period (LMP; 24 May–30 June) and social mobility period (SMP; 01 July–31 August), Upper Peninsula of Michigan, 2010 (light grey bars) and 2011 (dark grey bars)

greater occurrence of fawn hair in coyote scats during 2011 during LMP when fawn densities were less than 2010. Patterson et al. (1998) also found coyote consumption rates varied across years during summer but did not estimate prey densities. Our observed lack of functional response to changing fawn densities between 2010 and 2011 may be due to variation in abundance or availability of alternative prey during these years.

We identified that coyotes exhibited a functional response between LMP and SMP, consuming more fawns during LMP. During LMP fawns are small (<6 kg) and behavior is generally characterized by little movement (Ozoga et al. 1982); coyotes likely used this resource because fawns are within their predicted optimal prey range, being small, readily available, and come at a relatively low cost of capture compared to fawns in SMP or adult deer. Similarly, Lingle (2000) found that coyotes exhibited greatest predation of white-tailed deer fawns <8 weeks old when most vulnerable. Other carnivores such as arctic foxes (Eide et al. 2005), European polecats

(*Mustela putorius* [Lode 2000]), and harbor seals (*Phoca vitulina* [Middlemas et al. 2006]) appear to exhibit functional responses to prey species that are most available. O'Donoghue et al. (1998) found that as snowshoe hare densities varied coyotes consumption rates varied accordingly. We suspect the same would be true for coyotes consuming white-tailed deer, in that kill rates would remain constant unless prey densities or vulnerability changed. We observed a greater number of fawns consumed by coyotes during LMP and fewer consumed during SMP; these apparent reductions in kill rates suggest that coyotes responded functionally to decreasing fawn density while simultaneously fawns gained body mass and exceeded the predicted optimal prey size for coyotes.

Although number of fawn deer consumed by coyotes varied between LMP and SMP, biomass consumed was overall similar between periods. However, multiple parameters were estimated to calculate biomass and number of deer consumed, and it is possible that the variance or our estimates did not include the true biomass or number of deer consumed. Alternatively, percent of coyote energetic requirements met by fawn deer was considerably less during SMP than LMP, and we suggest observed similarities in fawn deer biomass consumed between periods is a consequence of reduced vulnerability of fawn deer and increased availability of alternate prey. During early summer coyotes have been found to begin eating ripening wild fruits (Morey et al. 2007) and the first birth pulse of small mammals occurs [e.g., snowshoe hare (Griffin and Mills 2009)], providing a greater food resource base for coyotes and possibly leading to decreasing fawn consumption rates. The similarity in adult deer biomass consumed between periods likely reflect similar numbers of individuals consumed during each period.

We observed relatively low and constant consumption of adult deer compared to fawn deer, suggesting fawns are more energetically advantageous (Nelson and Woolf 1987) and may be considered a separate prey source. Patterson et al. (1998) and Lingle (2000) also noted a lesser kill rate by coyotes on adult deer compared to fawns during fawning season, likely due to greater vulnerability of fawns. As predicted, we observed greatest coyote consumption of fawn deer during LMP and less during SMP and low consumption of adult deer during both periods. Our observations support a previous estimate of optimal prey size for coyotes based on carnivore body size (Carbone et al. 1999).

Many predatory species respond to pulsed resources through increased consumption of rapidly abundant prey (Careau et al. 2008; Yang et al. 2008). Coyotes quickly responded to the pulsed resource of fawn parturition with greater consumption rates of fawns during LMP, which declined as vulnerability and densities of fawns decreased

as their size and mobility increased. However, estimating densities of alternative prey sources and occurrence in coyote diet is necessary to better understand whether predators are exhibiting Holling's (1959) type II functional response to a particular prey or if a type III prey switching response is occurring (Patterson et al. 1998). We suggest that coyotes, a generalist carnivore, respond functionally to fawn parturition similar to many generalist carnivores responding to pulsed resource events (Reimchen 2000; Darimont and Reimchen 2002; Eide et al. 2005).

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