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Factors Affecting Elicitation of Vocal Response from Coyotes and Population-Level Response to a Pulsed Resource Event

Tyler Robert Petroelje

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Factors affecting elicitation of vocal response from coyotes and population-level response

to a pulsed resource event

By

Tyler Robert Petroelje

A Thesis
Submitted to the Faculty of
Mississippi State University
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in Wildlife, Fisheries and Aquaculture Science
in the Department of Wildlife, Fisheries and Aquaculture

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Factors affecting elicitation of vocal response from coyotes and population-level response

to a pulsed resource event

By

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Long-distance vocalizations by canids play an important role in communication among individuals. I evaluated efficacy of broadcasted coyote (*Canis latrans*) group-yip calls and gray wolf (*C. lupus*) lone howls to elicit vocal responses from 18 GPS-collared coyotes on 144 occasions. I concluded that eliciting coyote vocalizations where wolves are present will not bias responses, and recommend eliciting coyote vocalizations using recorded coyote group-yip howls during July–September to estimate species' presence or density.

From foraging theory, generalist predators should increase consumption of prey if prey availability increases. I estimated densities for coyotes, adult deer, and fawns, and collected coyote scat to estimate occurrence and biomass of adult and fawn deer consumed by coyotes during 2 periods. I suggest that consumption rates of coyotes was associated positively with increases in fawn density, and fawn consumption by coyotes follows predictions of foraging theory during this pulsed resource event.

DEDICATION

      I dedicate this research to my parents Kerry and Connie Petroelje for instilling me with a drive to work hard, and supporting my decisions through undergraduate and graduate school; and to my grandparents Robert and Georgia Arends for sharing with me their interest in the natural world

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

Coyotes (*Canis latrans*) and wolves (*C. lupus, C. lycaon*) are sympatric across

portions of their North American ranges (Paquet 1992). In addition to re-colonization of

wolves to Michigan's Upper Peninsula in 1989, coyote population trends indicate coyotes

are also increasing in abundance (Fig. 1). However, few reliable survey techniques exist

to estimate large carnivore abundance (Patterson et al. 2004). Identifying factors that

influence vocal responses from coyotes may improve utility of howl surveys as a

technique to estimate abundance where coyotes and wolves are sympatric. Evaluating

and improving this survey technique is important for management of coyotes as they may

affect prey species such as white-tailed deer (*Odocoileus virginianus*; Ozoga and Harger

1966, Whittaker and Lindzey 1999).

In contrast to coyote populations, white-tailed deer populations appear to be

declining in the western Upper Peninsula, and have failed to recover since the severe

winters of 1995 and 1996 (Fig. 1). As coyote predation has accounted for up to 80% of

fawn white-tailed deer mortality in some areas (Grovenburg et al. 2011), accurate

abundance estimates of coyote populations are important to understand the relationships

between these 2 populations. Predation by coyotes on white-tailed deer fawns would

likely be greater than predation on adults, due to greater vulnerability (Nelson and Woolf

1987) and smaller body size of fawns. The magnitude of predation on white-tailed deer

fawns and adults is important to understand the affect that coyotes have on deer recruitment in Michigan's Upper Peninsula.

My research was part of a larger study titled "Role of predators, winter weather, and habitat on white-tailed deer fawn survival in the south-central Upper Peninsula of Michigan". Research conducted included estimates of white-tailed deer fawn and adult female survival, assessed cause-specific mortality attributable to black bear (*Ursus americanus*), coyotes, wolves, and bobcat (*Lynx rufus*), and assessed effects of winter severity and habitat condition on predation rates, and white-tailed deer parturition and recruitment rates. My objectives were to quantify factors influencing elicitation of vocal responses from coyotes, estimate coyote abundance in the south-central Upper Peninsula of Michigan (Fig. 2) using howling surveys, and estimate coyote consumption rates of white-tailed deer during 2009–2011.
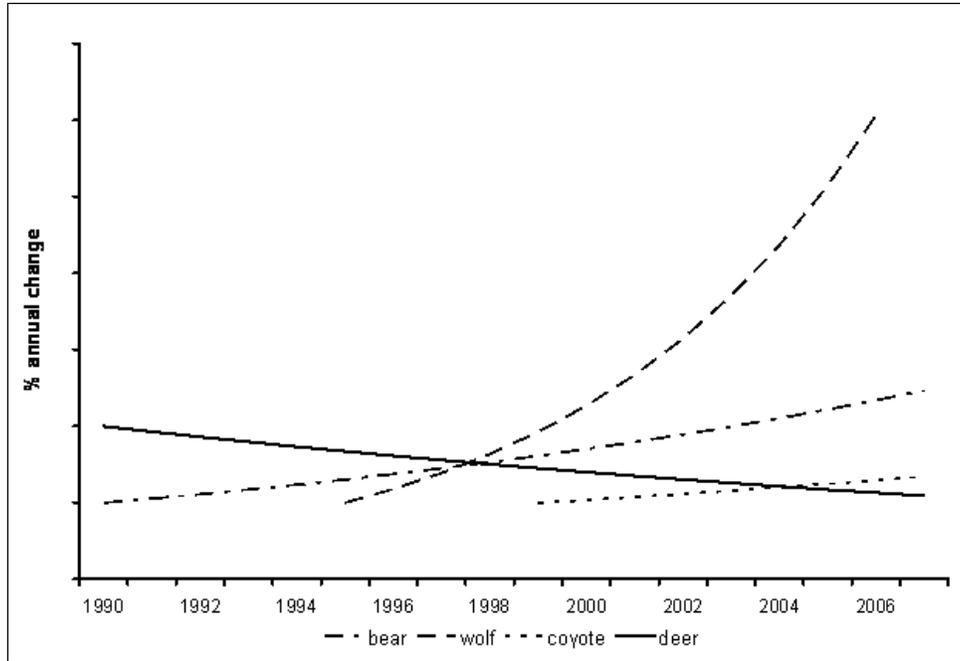
Figure 1   Percentage annual population change of black bear, wolf, coyote and
             white-tailed deer during 1990–2006, Upper Peninsula of Michigan, USA.

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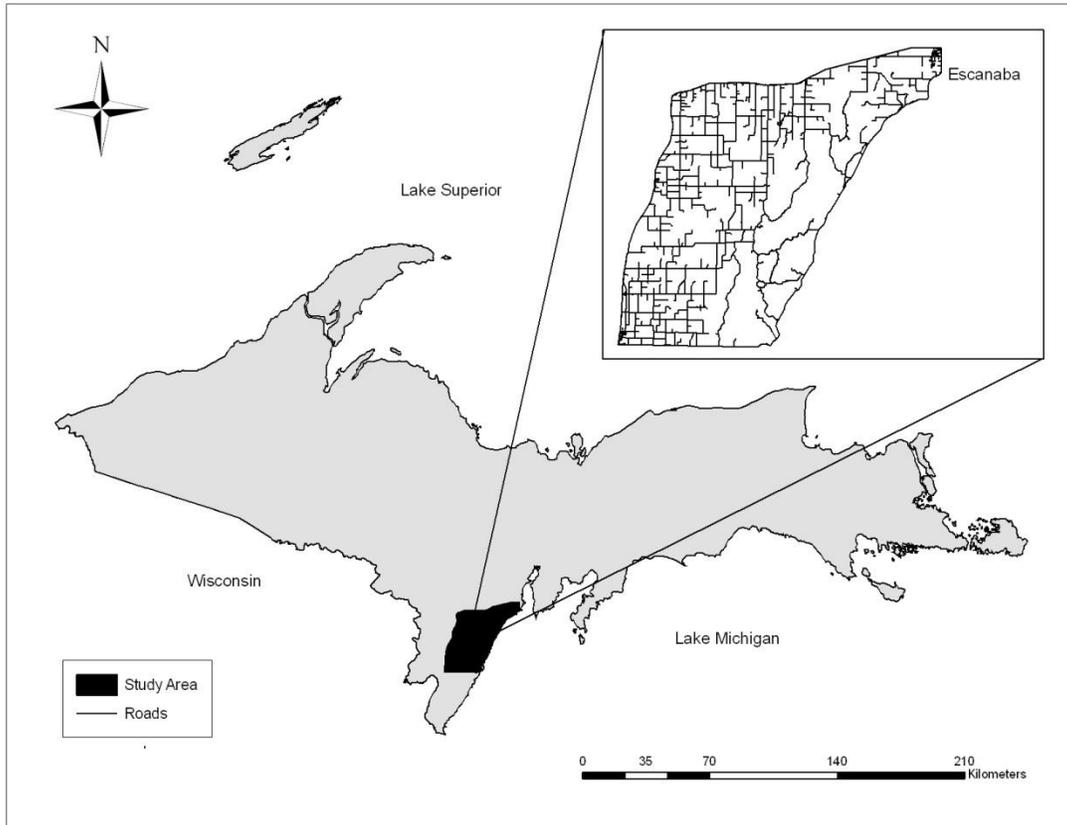
Figure 2   Location of study area (45.6° N, 87.4° E) with inset showing roads, Upper
                  Peninsula of Michigan, USA.

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CHAPTER II

FACTORS AFFECTING ELICITATION OF VOCAL RESPONSES FROM COYOTES

Canids use long-distance vocalizations for individual identification, communicating among pack members, and establishing territory boundaries between packs (Joslin 1967, Theberge & Falls 1967, Mitchell et al. 2006). Researchers have studied canid vocalizations since the 1970s to examine aspects of behavioral ecology (Laundré 1981, Harrington & Mech 1982, Walsh & Inglis 1989) and communication (McCarley 1975, Wenger & Cringan 1978, Lehner 1982, Okoniewski & Chambers 1984, Mitchell et al. 2006). In addition, wildlife managers have broadcasted coyote (*Canis latrans*) vocalizations to attract and remove problem coyotes (Lehner 1976, Coolahan 1990, Mitchell 2004). Other uses of broadcast stimuli to elicit vocal responses include estimating canid densities by dividing number of individuals or packs responding by area surveyed (Fuller & Sampson 1982, Dunbar & Giordano 2002), and monitoring status of re-colonizing gray wolves (*C. lupus* [Gaines et. al. 1995]).

Broadcast stimuli used to elicit canid vocal responses include sirens (Wenger & Cringan 1978, Pyrah 1984), human-simulated howling (Okoniewski & Chambers 1984, Fuller & Sampson 1988), and recordings of species-specific vocalizations (Lehner 1982, Mitchell et al. 2006). Human-simulated howling can be as effective as recorded howls for eliciting vocal responses from wolves (Joslin 1967); however, comparative work is not available for coyotes. A disadvantage of human-simulated howling for many applications

(e.g., monitoring status of canid populations) is variability in duration, frequency, and intensity of stimuli. Consequently, Lehner (1976) suggested using recorded broadcasts to standardize trials for eliciting responses.

Canid vocal responses include barks, group howls, and group-yip howls for coyotes (Lehner 1982), and lone howls and chorus howls for wolves (Harrington & Mech 1982, Gazzola et al. 2002). The group-yip howl appears most effective for eliciting calls from coyotes (Lehner 1982). Harrington & Mech (1982) recommended use of individual wolf howls that alternated between "flat" (single sustained frequency) and "breaking" (variable frequency) howls to reduce variation in response rate by packs of different sizes.

Using a single-species broadcasted call to detect multiple species would be useful if the call did not inhibit the response rate of any species. Non-vocal types of communication (e.g., urine-marking) may serve similar purposes (e.g., territory announcement) across canid species (e.g., wolves, coyotes, and red foxes [*Vulpes vulpes*]) including interspecific communication (Harrington 1981). Few studies have assessed efficacy of eliciting vocalizations of a canid using a sympatric canid species vocalization. Gaines et al. (1995) reported a greater response rate from coyotes (9.9%) than wolves (0.1%) using a human-simulated wolf howl, though this difference was likely due to low wolf density and not greater interspecific responsiveness from coyotes. By using collared individuals, one can estimate true response rates of coyotes to different call types.

Residency, gender, and geographic location of coyotes may affect response rate. Resident coyotes often howl to define territorial boundaries, whereas transients may

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display risk avoidance behavior by not vocalizing or approaching a broadcasted call (Mitchell 2004). Gender of resident coyotes may affect vocal response behavior; in a captive study of 4 coyote pairs, males vocalized more than females (Mitchell 2004). However, there is little information on free-ranging populations. Also, regional variation of breeding and dispersal behavior may affect peak times for elicitation. In the northeast United States (U.S.), greatest responsiveness occurred from late-summer to early-fall before dispersal (September–November [Okoniewski & Chambers 1984]) when territory announcement may be important. In the west and southwest U.S., pair formation and breeding (February–March) as well as late-summer and early winter (August and November) were periods of greater responsiveness (Laundré 1981, Walsh & Inglis 1989), whereas months of greatest responsiveness for the Midwest have not been reported.

Identifying factors that influence vocal responses from coyotes may improve utility of howl surveys as a technique to estimate abundance where coyotes and wolves are sympatric. I quantified vocal response rates of coyotes to two species-specific (one coyote, one wolf) broadcasted vocalizations and assessed importance of factors that may influence these responses. I hypothesized that response rates would increase from June–September, be greater for residents and males, and that both call types would elicit responses equally due to intraspecific and interspecific communication as coyotes and wolves (*Canis lupus, C. lycaon*) are sympatric in Michigan's Upper Peninsula.

Material and methods

Study area

I conducted this study in portions of Delta and Menominee counties in Michigan's Upper Peninsula (45.6° N, 87.4° E) encompassing about 870 km^2. Limestone bedrock,

ground moraine, cedar swamps, northern hardwood forests, and coastal marshes characterized the study area (Albert 1995). Land ownership consisted of private (74 %) and public (26 %) lands including the Escanaba River State Forest. Predominant land covers included 29% lowland deciduous (e.g., green ash [*Fraxinus pennsylvanica*], speckled alder [*Alnus incana*]), 17% upland deciduous (e.g., sugar maple [*Acer saccharum*], quaking aspen [*Populus tremuloides*]), 14% lowland conifer (e.g., black spruce [*Picea mariana*], balsam fir [*Abies balsamea]*) forests and 17% agriculture (e.g., row crops, hay fields, and pastures [Michigan Center for Geographic Information 2009]). Elevations ranged from 177 to 296 m. The western portion of the study area contained more agriculture and a rolling landscape. Temperatures ranged from average highs of 24.2° C during July to average lows of 7.4° C during September. Rainfall during June–September of 2009–2011 averaged 17.69 cm (*Escanaba, MI airport; Automated Surface Observation System, National Weather Service 2011*).

Data collection and analysis

Members of the Michigan Predator-Prey Project, Michigan Department of Natural Resources, and I captured coyotes and wolves during May–July 2009–2011 using #3 padded foot-hold traps (Oneida Victor, Cleveland, Ohio, USA) and MB-750 four-coil foothold traps (Minnesota Brand, Pennock, Minnesota, USA), respectively. Also, during March 2011, I captured coyotes using neck cable restraints (Etter & Belant 2011). I anesthetized coyotes and wolves with a ketamine (4 mg/kg and 10 mg/kg, respectively) and xylazine (2 mg/kg) mixture (Kreeger 2007). I administered yohimbine (0.15 mg/kg) as a reversal for xylazine before I released animals at their capture sites (Kreeger 2007). Prior to release, I recorded gender, weight, applied ear tags (Rototags, Nasco Farm

Supply, Fort Atkinson, Wisconsin, USA), and inserted a passive integrated transponder tag (Avid, Norco, California, USA) subcutaneously between scapulae of all individuals. I injected each coyote and wolf with oxytetracycline (0.074 ml/kg) or penicillin (0.074 ml/kg) as an antibiotic. I fitted coyotes and wolves with a global positioning system (GPS) collar with a very high frequency (VHF) transmitter (Model GPS7000SU, Lotek Wireless, Newmarket, Ontario, Canada). I programmed the GPS collars to acquire and store locations every 15 minutes. I flew in an aircraft 1–2 times weekly to upload collar location data using ultra high frequency communication and a handheld command unit (Lotek Wireless Inc., Newmarket, Ontario, Canada). Mississippi State University Institutional Animal Care and Use Committee approved all capture and handling procedures (protocol 09-004).

I tested two species-specific calls (one coyote, one wolf) to identify the call type most likely to elicit coyote responses as well as factors that may affect response rate of individuals to each call type (e.g., residency, gender, month [Laundré 1981, Okoniewski & Chambers 1984, Mitchell et al. 2006], and presence in known wolf territory). I elicited vocalizations during August–September 2009 and June–September 2010–2011 from dusk to 0300h (Harrington & Mech 1982, Okoniewski & Chambers 1984). I located collared coyotes monthly using a VHF receiver and 3-element yagi antenna and exposed them to one of the calls at random for the first howling trial. I relocated and attempted to vocally elicit collared coyotes up to 4 times monthly, alternating the call type to limit the possibility of habituation (Wenger & Cringan 1978).

I used a FX3 game caller (FoxPro, Lewiston, Pennsylvania, USA) to broadcast coyote and wolf calls. Using only the front speaker to minimize distortion, I oriented the

game caller vertically about 2.2 m above ground to broadcast omnidirectionally. I

broadcasted calls at 105dB, similar to the volume of coyote vocalizations (Mitchell et al.

2006). I elicited vocalizations when wind speed was <12 km/h (Kestrel 1000 weather

meter [Nielsen-Kellerman, Boothwyn, Pennsylvania, USA]) and there was no

precipitation, as these conditions can inhibit responses or identification of responses

(Harrington & Mech 1982). I broadcasted coyote group-yip howls (20 sec) or 5 lone wolf

howls, alternating between flat and breaking (5–7 sec each), followed by a 90 second

listening period. I repeated this process 3 times. I attempted to record coyote vocal

responses using a Sennheiser MKH 70 shotgun microphone (Sennheiser Electronic,

Wennebostel, Germany) attached to a laptop computer through a two-channel analog

audio to digital audio mixer (US-144mkII [Tascam, Montebello, California, USA]). I

used Audacity® audio recording software (v. 1.3.12, Audacity Team 2011) to record

digitized vocalizations at a 24-bit/96 kHz sampling rate. I classified recorded coyote

responses as a bark, bark-howl, lone howl, group howl, or group-yip howl (Lehner 1978)

and whether responses were from individual coyotes or groups (>2 coyotes). I recorded

each telemetered coyote detected as moving or stationary (Okoniewski & Chambers

1984) using 2 (15 min) GPS locations (obtained from collars) immediately preceding

each howling trial. I recorded coyote response behavior (i.e., approaching, retreating, or

stationary) to each broadcast by using 2 (15 min) GPS locations obtained from collars

immediately following each howling trial.

I considered coyotes residents if their seasonal range (May–September) did not

overlap ranges of other coyotes as seen in transient individuals (Kamler & Gipson 2000).

I used seasonal ranges of GPS collared wolves to determine when collared coyotes were

in known wolf territories during a broadcasted trial. I calculated seasonal ranges for coyotes and wolves using a 95% fixed kernel density estimate with *ad hoc* smoothing parameter using package adehabitatHR (v. 0.3.3) in Program R (v. 2.13.1, R Foundation for Statistical Computing, Vienna, Austria http://www.r-project.org).

Researchers have detected coyote responses to broadcasted calls from up to 2 km in habitat similar to my study area (Wolfe 1974). To assess audible distance of elicited calls and identify if a collared individual was responding, I estimated distances of collared coyote responses by comparing their GPS collar locations with the broadcast locations nearest to the time of the elicited response, or broadcasted call if no response was observed, using ArcGIS® (v. 10.0, ESRI, Redlands, CA, USA). I compared the bearing from the broadcast location to the GPS collar location (obtained using ArcGIS) to the bearing obtained with the directional antenna. I assumed the response was from a different individual if these bearings differed by >5º.

I used mixed effects logistic regression models (LOGIT) to estimate which factors influenced coyote responses to broadcasted vocalizations (R package lme4, v. 0.999375–42). The response variable was elicited coyote vocalizations per trial (i.e., response or no response) and explanatory variables included month, presence of collared coyote within known wolf territory, call type broadcasted (coyote group-yip or wolf howl), gender, and residency status (resident or transient) of collared individuals. I used an independent LOGIT which included distance, call type, coyote movement preceding each broadcast, and coyote response behavior following broadcasts as explanatory variables, as only 91 of 144 observations included associated GPS data. I included year and individual coyote as random effects and calculated standard error (SE) and upper and lower 95%

confidence interval for each estimated parameter for each model. I used a least square differences multiple range test to discern differences in response rates across months, and a power analysis test (R package pwr, v. 1.1.1) to verify adequate power of my inferences. Statistical power was sufficient for analyses conducted and statistical significance was set at $\alpha = 0.05$.

Results

From 2009 to 2011, I captured and collared 25 coyotes, of which 18 (11 male, 7 female) were located and exposed to broadcasted howls. I captured and collared 8 wolves to determine wolf territories (June–September) within the study area that ranged from 38 to 837 km^2 in size. Overall, I exposed the 18 coyotes to a coyote group-yip call 12, 14, 28, and 23 times from June to September, respectively, and a lone wolf call 14, 11, 20, and 22 times from June to September, respectively. Coyote response rate was greater ($P < 0.05$) in August than June; however, response rates during July and September were neither greater than June ($P > 0.05$) nor less than August ($P > 0.05$). Responses were elicited at 37 of 144 howling trials (response rate = 25.7%) and included one bark, 14 bark-howls, 2 lone howls, 3 group howls, and 17 group-yip howls. Group responses occurred at 53% and 55% of male and female trials, respectively. Coyote activity level (i.e., moving or stationary) at time of broadcast did not influence vocal response from individuals ($P = 0.691$, SE = 0.757).

Male and female response rates were similar (Table 1). Resident ($n = 13$) and transient ($n = 5$) coyotes had average seasonal ranges of 16 km^2 (SD = 5.7 km^2) and 183 km^2 (SD = 70.7 km^2), respectively. Resident coyotes (31%) responded 3 times more frequently than transient individuals (10%); transients vocalized only during August (Fig.

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3). I noted wolves responded during 3 broadcasted lone wolf call howling trials, twice followed by non-target coyote response. Broadcasted calls in ($n = 25$) and out ($n = 119$) of known wolf territories elicited similar coyote response rates ($P = 0.896$, SE = 1.143); there was no interaction between resident coyote response rates in and outside of known wolf territories.

Calls were broadcasted at distances of 0.24–4.69 km ($\bar{x} = 1.32$ km, $n = 91$) and elicited responses were detected at distances of 0.26–2.85 km ($\bar{x} = 0.94$ km, $n = 21$). I found no correlation (positive or negative) between response rate of coyotes and distance, and there was no interaction between call type and distance of response (Table 1). Coyotes responded similarly to both broadcasted calls at distances <2.0 km (Fig. 4), and only one response was elicited with a coyote group-yip howl at a distance greater than 2.0 km. Coyotes were more likely to respond ($P = 0.048$, SE = 1.67) when they moved toward broadcasts of a lone wolf howl compared to responding when stationary and a coyote group-yip howl was played.

Discussion

Vocal response by coyotes to broadcasted calls was greatest from residents, in or outside of wolf territories, during August, and was not influenced by call type. I expected a greater response rate in August–September because long distance vocalizing becomes more important as pups mature and pack members become more spatially dispersed (Harrington & Mech 1979). The low responsiveness of resident individuals during June (5.6%) was similar to findings by Laundré (1981) and Gaines et al. (1995), where responses in June were less than August. When pups are young (i.e., June) long distance vocalizations may not be necessary, or may pose a greater risk to young at den sites.

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Individual variation and repeated trials on the same individuals also may affect responsiveness across months. Although I attempted to minimize potential for habituation by alternating calls and limit repeated trials, I exposed individuals to the same calls, which could have caused habituation (Wenger & Cringan 1978) and potentially reduced response rates in later months. Thus, my reported response rates may be conservative.

Apparent male and female response rates were similar. However, for resident collared males and females it was unknown which group individuals were actually responding; 48.6% of responses were group responses and either pair member could have initiated responses. Similar to Gese & Ruff (1998) I was unable to determine if a conspecific group member was present and initiated responses. However, Mitchell (2004) identified that captive paired females were more likely to respond after a male initiated a response which may have influenced response rates of free-ranging females if they followed the same pattern.

I observed a lesser response rate for transient coyotes, which may be due to risk avoidance behavior toward territorial coyotes or lack of territory to defend (Harrington & Mech 1979, Gese & Ruff 1998). Assuming equal capture probability, transients comprised 28% of my sample population, similar to Gese et al. (1988) where 22% of coyotes were transient. When conducting broadcast elicitation surveys, residents are more likely to respond, but additional individuals likely exist in the population as non-responding transients and wildlife managers should adjust estimates of abundance to include them. If I consider 25% of the population to be transient and their response rate to be 1/3 of residents, it may be appropriate to inflate survey estimates by 16.7%.

Howling appears to serve similar purposes (e.g., territory maintenance) for wolves and coyotes (Theberge & Falls 1967, Gese & Ruff 1998) and the observed equal response rate of coyotes to both calls at distances <2.0 km and within or outside of known wolf territories suggests coyotes may perceive lone wolf vocalizations as a non-threatening interspecific communication. Coyotes would likely reduce vocalizations or would move away from broadcasts if coyotes perceived wolf calls as a predation risk. My observations of coyotes moving toward lone wolf broadcasts after responding suggests these individuals did not perceive lone wolf call broadcasts as a high risk at distances observed. Given my results of similar coyote response rates to broadcasted coyote and wolf vocalizations, a lone wolf howl may be an effective technique to estimate simultaneously, presence or abundance of both species.

Distance from broadcasted calls to coyotes may influence vocal response rates. I observed coyotes (collared and non-collared) approach on 5 occasions after broadcasting without vocalizing. Broadcasting calls close to coyotes using a coyote group-yip or lone wolf call may limit vocal responses due to vocalizations being of high risk when close to a conspecific or wolf, or long distance vocalizations may not be necessary when individuals are close. I heard coyote responses to broadcasted vocalizations from distances similar to those observed by Fuller & Sampson (1988). By sampling locations $\geq$4.0 km apart, double-counting individuals during a survey would be unlikely. Most calls were elicited at 0.5–2.0 km (86%), and although coyotes likely hear calls at farther distances (Lehner 1982), likelihood of hearing a response from >2.0 km appears low, especially in densely forested habitat.

It is important to identify factors that influence or are associated with response rates to improve precision of surveys and reduce number of surveys to confirm presence or absence of coyotes when response is low. Because transient coyotes may represent a substantial proportion of the population, abundance estimates based on broadcast elicitation should account for differences in response rates by resident and transient individuals. I recommend using recorded coyote vocalizations to elicit coyote responses as associated equipment is of low cost, easy to transport, and recordings provide consistent and high-quality broadcasts. I recommend conducting surveys for coyotes in the Upper Peninsula of Michigan during July–September and sampling locations ≥4.0 km apart to increase response rates and decrease probability of double-counting individuals for more precise estimates of abundance or density. I conclude that coyote surveys conducted in areas of sympatric wolves will not be biased by low response, as coyotes did not reduce vocal response rates within known wolf territories.

Table 1   Estimated parameter effects on coyote vocal response to broadcasted coyote and gray wolf calls, August–September 2009 and June–September 2010–2011, Upper Peninsula of Michigan, USA.

Parameter[a]	Estimate	95% Confidence Interval Lower	95% Confidence Interval Upper	z-value	P
MONTH [July][b]	2.05	-0.24	4.34	1.76	0.079
MONTH [August][b]	2.38	0.25	4.51	2.19	0.029
MONTH [September][b]	2.06	-0.08	4.19	1.89	0.059
CALLTYPE [Wolf lone howl][b]	-0.11	-0.94	0.72	-0.26	0.794
GENDER [Female][b]	-0.50	-1.49	0.49	-0.98	0.325
RESID [Resident][b]	1.55	0.00	3.11	1.96	0.050
WOLF TERRITORY [In][b]	0.15	-2.09	2.39	0.13	0.896
WOLF TERRITORY [In] × RESID [Resident][b]	-1.30	-4.48	1.89	-0.80	0.425
DISTANCE[c]	-0.71	-1.59	0.17	-1.58	0.115
CALLTYPE [Wolf lone howl][c]	1.41	-1.43	4.26	0.97	0.330
MOVING [Yes][c]	0.30	-1.18	1.78	0.40	0.691
MOVERESP [Toward][c]	-0.12	-2.03	1.79	-0.12	0.903
MOVERESP [Away][c]	0.99	-0.80	2.78	1.09	0.277
DISTANCE × CALLTYPE [Wolf lone howl][c]	-2.61	-5.99	0.77	-1.52	0.130
CALLTYPE [Wolf lone howl] × MOVERESP [Toward][c]	3.30	0.03	6.57	1.98	0.048
CALLTYPE [Wolf lone howl] × MOVERESP [Away][c]	-1.73	-4.98	1.52	-1.05	0.296

[a] Reference categories include month = MONTH [June], residency status = RESID [transient], call type = CALLTYPE [coyote group yip], gender = GENDER [Male], and wolf territory = WOLF TERRITORY [Out], movement = MOVING [No], movement after broadcast = MOVERESP [Neither direction].
[b] Estimated with 144 observations and 37 responses.
[c] Estimated with 91 observations and 21 responses.
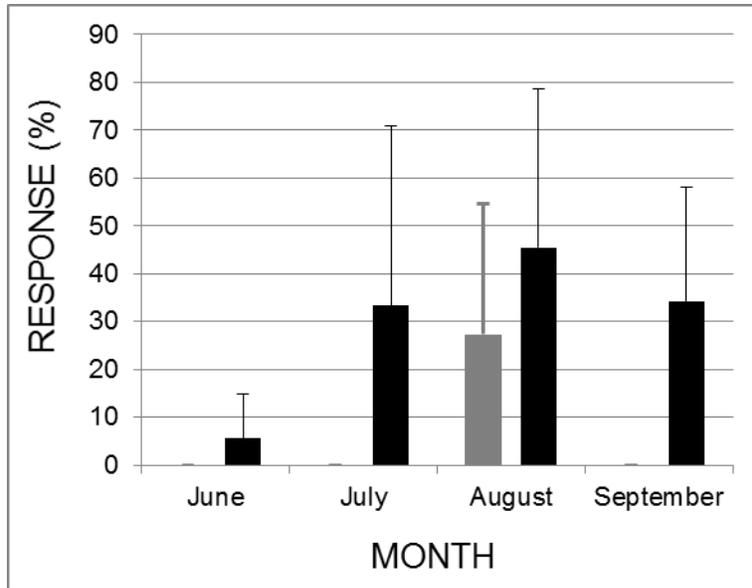
Figure 3   Resident (black) and transient (grey) coyote response rates to broadcasted coyote and gray wolf calls (+ standard deviation), August–September 2009 and June–September 2010–2011, Upper Peninsula of Michigan, USA.
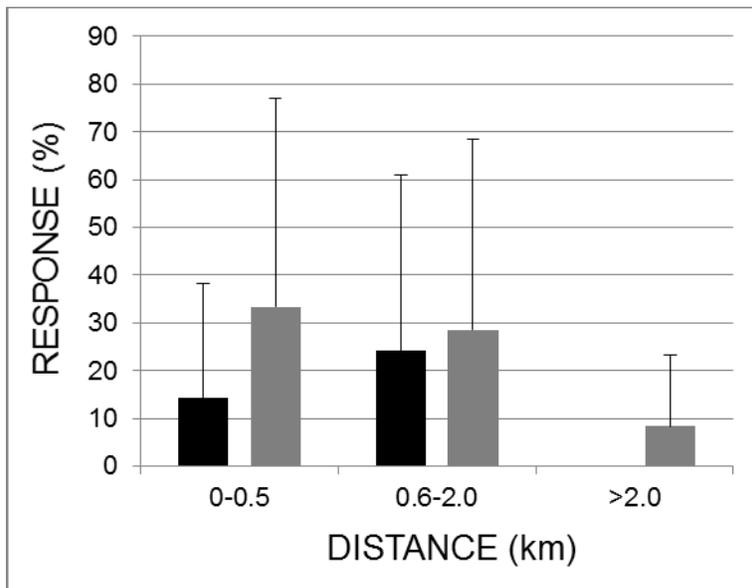
Figure 4   Proportion of coyote responses to broadcasted coyote (grey) and wolf (black) calls (+ standard deviation), August–September 2009 and June–September 2010–2011, Upper Peninsula of Michigan, USA.

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CHAPTER III

POPULATION-LEVEL RESPONSE OF COYOTES TO A PULSED RESOURCE

EVENT

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 I 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). 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 ≤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*) 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 ≤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 Hargar 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 one 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 Wolf 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.

I examined consumption response of a generalist predator to a pulsed resource event. Specifically, I estimated population-level consumption rates of fawn and adult white-tailed deer by coyotes and compared consumption rates across years. I 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. I predicted greatest consumption of fawns by coyotes would be near peak parturition. I 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, I predicted coyotes would consume fewer and relatively constant numbers of adult deer.

Material and methods

Study area

The study area included about 850 km^2 in Delta and Menominee counties in Michigan's Upper Peninsula (45.6° N, 87.4° E; Fig. 5) 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

I divided the study area into 4 survey sections with 55 non-overlapping survey points (Fig. 5). I 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 km^2 (81%) of the study area. I conducted howl surveys from dusk until 0300 h, August–September 2009 and July–September 2010–2011. Each month I 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. I 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. I did not conduct howl surveys during weeks 3–4 to limit potential habituation to broadcasted calls (Wenger and Cringan 1978). I attempted to

visit all survey points in each survey section in one night such that I completed each howl

survey in 4 consecutive nights, weather permitting. I 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, I aurally estimated number of individuals

responding within a pack. I 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

      I 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) I modeled abundance

of each site (N_i) fit to a Poisson distribution. I 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, I related heterogeneity in N_i to heterogeneity in p_i following Royle and Nichols

(2003) where:

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

      In this case, I used p_i when constructing likelihood of detection while accounting

for heterogeneity across the landscape (see Royle and Nichols 2003).

      I 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 or non-detection of individuals at each survey point. I included a time dependent variable to observe if detection changed during survey months (July–September) and a habitat variable (i.e., % forest cover [upland and lowland coniferous and deciduous forests combined] and agriculture; Fry et al. 2011) to discern if abundance varied across habitats. I 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.

I 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 [Table 2]). I considered models with lesser AIC$_c$ scores as better models; however, I 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 I used density estimates from top-ranking models only to extrapolate to non-surveyed portions of the study area.

Deer abundance estimates

I used estimates of adult and fawn white-tailed deer abundance and density obtained within 249 km^2 of the central portion of my study area (Duquette et al. *in review*) and assumed this was representative of my study area. Duquette et al. (in review) used 55 remote cameras 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 (Duquette et al. *in review*). Thus, I did not use any landscape variable to account for variation across my 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/km^2 (S.E. = 1.49), 3.7/km^2 (S.E. = 1.37) in 2010, and 3.3/km^2 (S.E. = 0.48) in 2011. Fawn density in 2009 was 0.6/km^2 (S.E. = 0.25), 1.3/km^2 (S.E. = 0.50) in 2010, and 0.8/km^2 (S.E. = 0.19) in 2011.

Scat collection and analysis

I 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 my analysis. I considered scats with adjacent coyote tracks as coyote scats (Prugh and Ritland 2005). For scats not associated with tracks I 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). I placed coyote scats in plastic bags and labeled each sample with location, date, and if coyote tracks were present.

I washed scats in nylon bags so that only hair, bone fragments, and hooves remained, and then dried these contents (Johnson and Hansen 1979). I 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. I 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. I 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. I 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, I 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

I 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 (~$2.0–2.5 \times$ basal metabolic rate; Laundraè and Hernadaz 2003) to calculate daily field metabolic rate. Laundraè and Hernandez (2003) found mated male and female coyotes had annual increased caloric requirements compared to un-mated individuals. I assumed a 50:50 coyote gender ratio, with 53% of the population being adult (average value from Knowlton 1972, Gese 1989). I assumed 54% of the adult female population had dependent young (Knowlton 1972) during both periods and mated individuals (male and

female) had to supply pups with 540.7 kcal/day during this time (Laundraè and Hernadaz 2003). Thus, I calculated energy requirements for 54% and 46% of the adult coyote population using mated (186.2 kcal/kg$^{0.75}$ + 540.7 kcal/day, male and 189.1 kcal/kg$^{0.75}$ + 540.7 kcal/day, female) and un-mated (185.6 kcal/kg$^{0.75}$ day) daily caloric requirements, respectively.

To estimate mean coyote body mass used in my calculations of energetic requirements, I 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). I 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). I recorded gender, morphometrics, applied ear tags, and weighed each individual. I administered yohimbine hydrochloride (0.15 mg/kg; Yobine, Ben Venue Laboratories, Benford, Ohio, USA) as a reversal for xylazine (Kreeger and Arnemo 2007) before I released coyotes at their respective capture sites. I received approval for all capturing and handling procedures through Mississippi State University's Institutional Animal Care and Use Committee (protocol 09-004).

I used mean coyote body mass to estimate daily field metabolic rate with Laundraè and Hernadaz's (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.

I 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. I

used deer captured during 2009–2011 to estimate mean body mass of adults ($\geq$ 1.5 years

old, n = 101, $\bar{x}$ = 66.3 kg, SD = 13.9) and date of parturition as well as body mass of

fawns (Table 3) 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, I 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.

I 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:

$$B_x = \frac{T_x n (C_x \alpha_x)}{K_x} \tag{2}$$

where B_x represents biomass of adult (N_A) or fawn (N_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 I 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

I observed an overall 24% coyote response rate and elicited responses at 34, 43, and 43 sites during 2009–2011, respectively. From aural responses, I estimated a mean of 46 and 56 coyotes responding during 2010 and 2011 surveys, respectfully. I was 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). I 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% (S.E. = 4.7) in 2010 and 6.2% (S.E. = 4.2) in 2011, respectively. Estimated coyote density during 2010 and 2011 was 0.37/km^2 (0.21–0.54 95% CI) and 0.32/km^2 (0.17–0.47 95% CI), respectfully. Abundance estimates for the entire study area were 314 (179–459 95% CI) coyotes in 2010 and 272 (145–400 95% CI) coyotes in 2011.

Scat analysis

I analyzed 149, 139, and 76 coyote scats for presence of fawn and adult deer hair during 2009–2011, respectively. 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, respectfully (Fig. 6). 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. 7) 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 12.8 kg (SD = 2.1 kg, n = 25). I calculated daily field metabolic rate as 1,800.7 kcal (186.2 kcal × 12.8 kg$^{0.75}$ + 540.7 kcal), 1,820.4 kcal (189.1 kcal × 12.8 kg$^{0.75}$ + 540.7 kcal), and 1,256.0 kcal (185.6 kcal × 12.8 kg$^{0.75}$) for male and female breeding and all non-breeding individuals, respectfully. Estimated body mass of fawns at birth were almost two times greater in 2010–2011 than in 2009 (Table 4).

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. 8a). 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. 8b). 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.

8c). Coyotes consumed 16.4 and 74.4 times more fawns than adult deer during LMP in

2010 and 2011, respectfully. In contrast, coyotes consumed 8.3 to 5.3 times more fawns

than adult deer during SMP in 2010 and 2011, respectfully.

Discussion

I 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*; Careau 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 I observed occur in

coyote response to fawn parturition (Fig. 7). Patterson et al. (1998) noted prey switching from snowshoe hare to fawns with onset of white-tailed deer parturition, and similar to my 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, I was not able to detect if coyotes exhibited a functional response in fawn consumption between years. 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 $0.6/km^2$, <50% of 2010 and 75% of 2011 estimates, proportion of fawn hair found in scat also was less. However, I observed a 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. My 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.

I 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

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harbor seals (*Phoca vitulina*; Middlemas et al. 2006) appear to exhibit functional responses to prey species that are most available. O'Donoughe et al. (1998) found that as snowshoe hare densities varied coyotes consumption rates varied accordingly. I 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. I 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 my 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 I 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.

I 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, I observed greatest coyote consumption of fawn deer during LMP and less during SMP and low consumption of adult deer during both periods. My 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). I 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).

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[1]	Model parameters	AIC_c	ΔAIC_c[2]	Wt[3]
2010	~int ~int	2	366.7	0	0.64
	~int ~forest + agri	4	367.9	1.22	0.34
	~date ~int	3	373.4	6.73	0.02
	~date ~forest + agri	5	374.7	7.97	0.01
2011	~int ~int	2	379.5	0	0.92
	~int ~forest + agri	4	384.9	5.47	0.06
	~date ~int	3	386.8	7.33	0.02
	~date ~forest + agri	5	392.3	12.82	<0.01

[1.] Model parameters included habitat (forest = % of each site that was forested, agri = % 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).
[2.] Difference between first model and selected model AIC_c scores.
[3.] Akaike weight; proportion of support for each model.

Table 3   Percentages 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	Percentage of scats		
		2009	2010	2011
Fawn	LMP	34	43	79
	SMP	19	26	21
Adult	LMP	22	23	9
	SMP	21	13	14

Table 4   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.
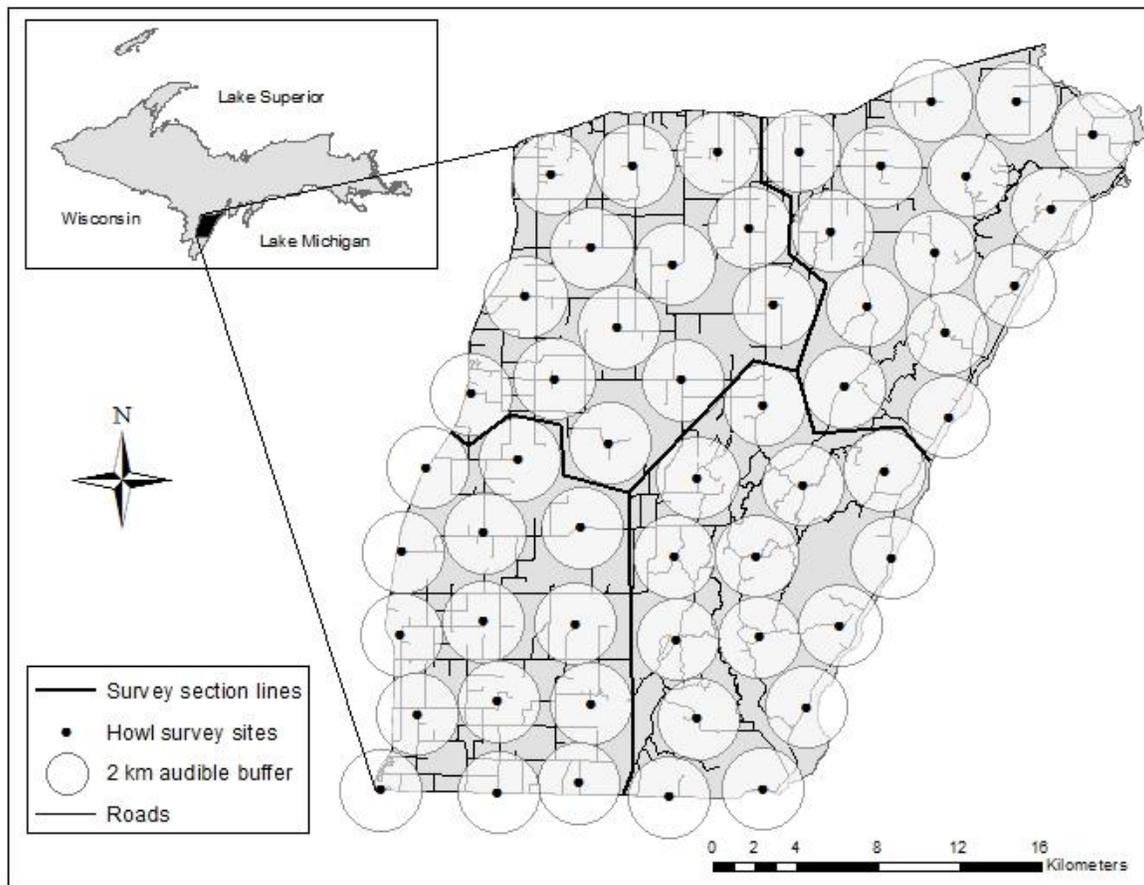

Figure 5   Locations of 55 howl survey sites with 2 km buffers for detecting coyote
            vocal responses in 4 survey sections, Upper Peninsula of Michigan, 2009–
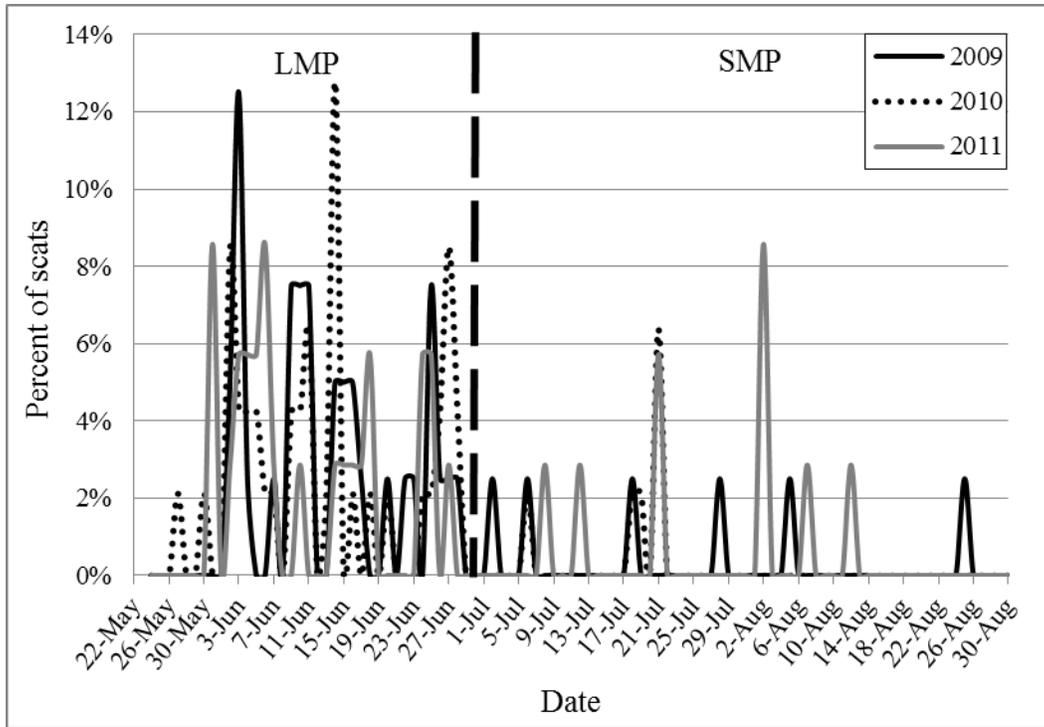   2011.

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Figure 6   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.
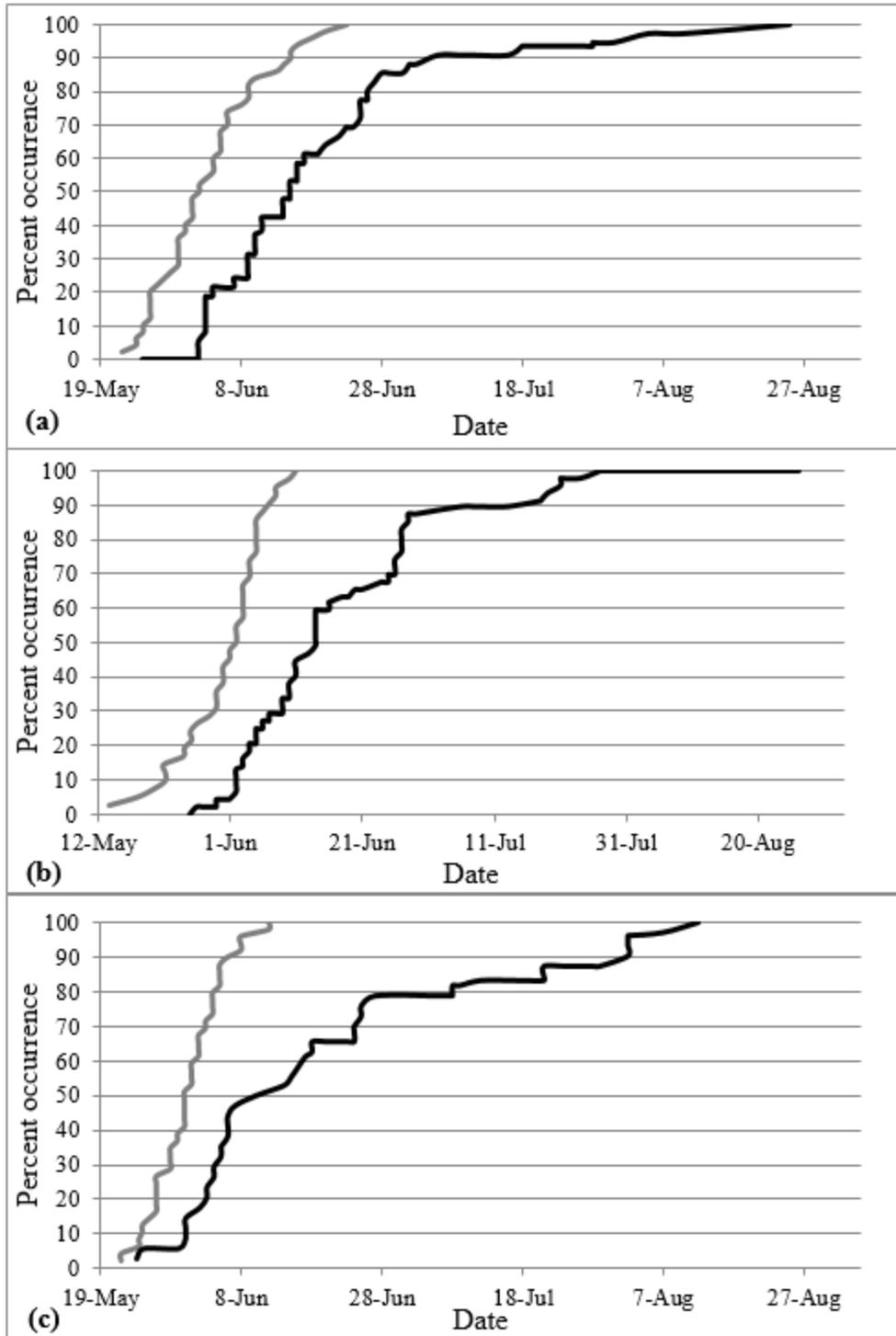
Figure 7   Comparison of cumulative percent occurrence of captured white-tailed deer
           fawns born (grey line [Duquette et al. 2011]) and cumulative percent
           occurrence of coyote scats with fawn hair by date (black line) for 2009 (a),
           2010 (b), and 2011 (c).

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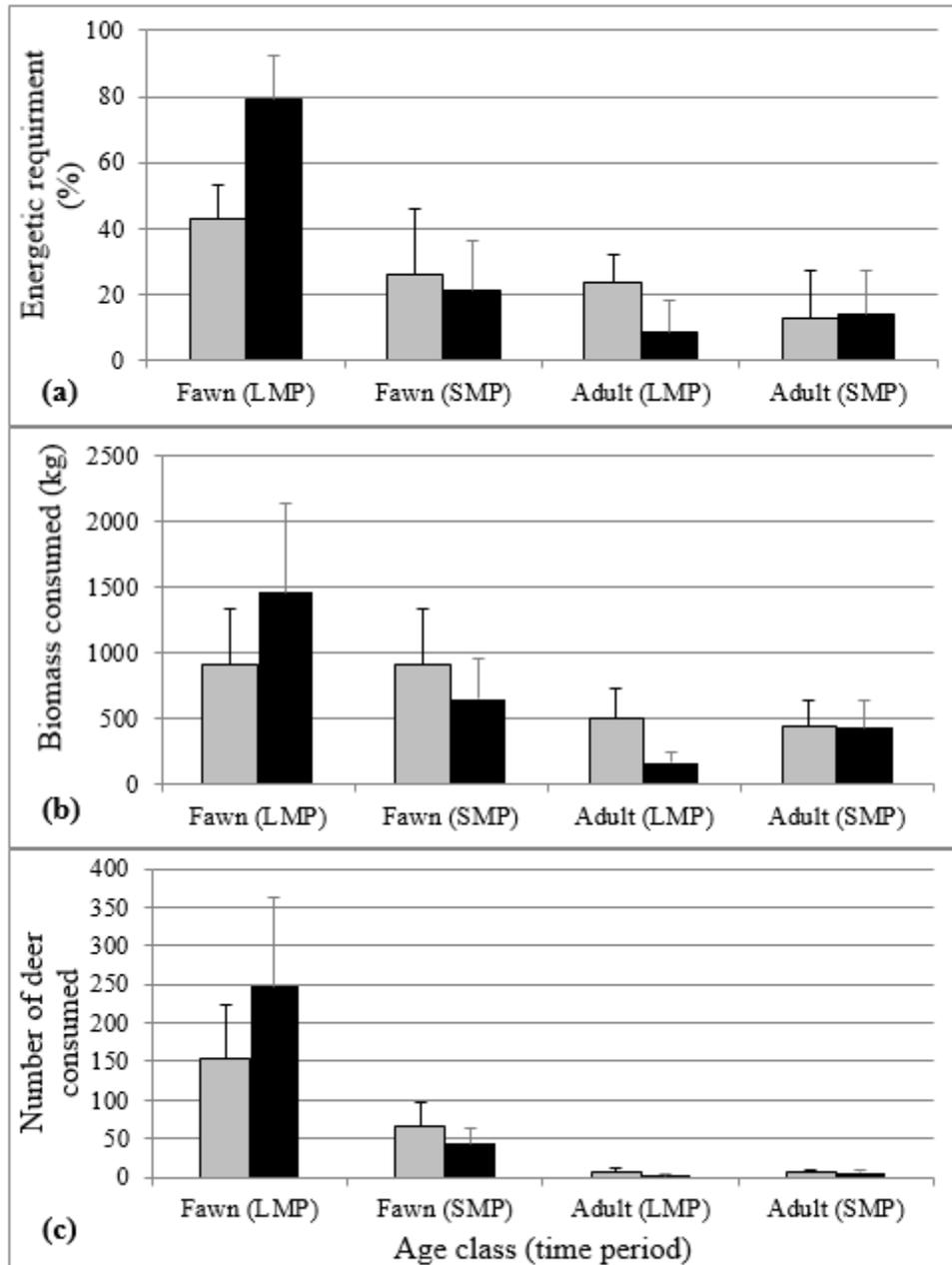Figure 8   (a) Estimated percentage of coyote energetic needs acquired from white-
tailed deer, (b) estimated biomass of deer consumed by coyotes, and (c)
estimated number of deer consumed by coyotes (+ 95% confidence
intervals) during fawn limited mobility period (LMP; 24 May–30 June) and
social mobility period (SMP; 01 July–31 August), Upper Peninsula of
Michigan, 2010 (grey bars) and 2011 (black bars).

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CHAPTER IV

CONCLUSIONS

Few techniques to estimate abundance of large terrestrial carnivores are available

(Patterson et al. 2004). As a management technique, howl surveys are not commonly

used to assess canid abundance (Gains et al. 1995). However, with advances in

occupancy modeling (Royle and Nichols 2003) howl surveys can provide population

estimates for coyotes (*Canis latrans*) over a large area that are cost effective, and surveys

conducted during July–September $\geq$4.0 km apart that account for non-responding

transient population will be most effective. In areas where coyotes and wolves (*Canis

spp.*) are sympatric, a single broadcasted call may allow monitoring both species

simultaneously, further enhancing cost effectiveness and applicability for estimating

abundance. As coyote abundance indices have been increasing in the Upper Peninsula of

Michigan (Fig. 1), it will become increasingly important for managers to survey and

monitor coyote populations, as they can have the potential to effect recruitment of prey

populations such as white-tailed deer (*Odocoileus virginianus*).

Just as monitoring coyote populations is important, understanding their effect on

prey populations, such as white-tailed deer, also is of interest to managers. In Michigan's

Upper Peninsula, white-tailed deer have considerable ecological, social, and economic

value as sport hunters spend >$600 million in Michigan annually. In my study coyotes

consumed significantly less adult deer than fawns during May–August, thus during this

time they likely effected potential recruitment more than adult survival. Further, coyotes responded functionally to white-tailed deer parturition, by increasing consumption of a readily-available resource (i.e., fawns) whereas adult deer consumption remained constant. However, to better understand the magnitude of coyotes effect on recruitment of white-tailed deer, alternative prey densities and their proportion in coyote diet also is needed (Patterson et al. 1998). In Michigan's Upper Peninsula it appears coyotes have the greatest potential to affect white-tailed deer recruitment soon after parturition, and reduce their consumption of neonates as fawns mature.

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