

Predator impacts on deer are goal of research efforts to begin in 2010

MADISON – Scientists with the Department of Natural Resources and the University of Wisconsin will launch an ambitious, multi-year field research effort to better understand the impacts predators such as wolves, bears, coyotes and bobcats have on white-tailed deer in Wisconsin.

A review of existing literature on predation and a mathematical analysis using Wisconsin's extensive harvest and population data suggest a low level impact, but just how much, at what times, by what predators and under what conditions are all relatively unknown at this time, scientists said.

“The literature review and data analysis are first steps that identified the need for specific field research on deer predation and how that research might be designed,” said DNR research scientist, Christopher Jacques.

A particular concern being raised by hunters is the fact of expanding wolf and bear populations in Wisconsin. Both are large predators that feed on deer either primarily as in the case of wolves or occasionally as in the case of bears.

*White-tailed deer in Buffalo County, photographed from DNR plane in February.
WDNR Photo by Jason Fleener*

Some hunters argue an expanded wolf population, in particular, has resulted in fewer deer in the northern and central forests.

Review of published research and preliminary data analysis suggests bears are having a small but measurable impact on fawn mortality and that wolves have a small impact on the mortality rate of adult does.

One study in northern Wisconsin will use radio telemetry to track fawns and determine how many are killed by predators and by which predators. Almost nothing is known, for example, about the impact of coyote and bobcat predation on deer in Wisconsin. Similar research is underway in Michigan's Upper Peninsula, and the two states are sharing results.

Another study, set to run for five years, will use a combination of field research methods, including radio telemetry, to study buck mortality. This research, on the DNR wish list for more than a decade, was recommended by independent auditors in 2006 to fine tune Wisconsin's procedures for estimating herd size.



The review of published research on predation and the early analysis of Wisconsin data were done by researchers Jacques of the DNR Bureau of Science Services and Tim Van Deelen of the University of Wisconsin- Madison. They unearthed 90 studies from the U.S. and Canada, most conducted in recent years with a few dating back to the 1960s and 1970s.

Many deer hunters tend to believe that every deer killed by a predator results in one less deer available for a human hunter to harvest. Research has found the truth to be more complicated. Predators do not, in fact, always reduce the population growth rates of prey.

Biologists use the terms “compensatory” and “additive” to describe the impact of predation on any given wildlife population. If predation is “compensatory,” it means the total number of prey to die in any given year does not change as a result of predation. It means the predators remove the number of animals that would have been lost anyway to other causes.

If predation is “additive,” then the predator is killing prey animals that otherwise would have survived the cycle of seasons. In these cases, the predator is slowing the growth of the prey population, or in some instances, causing that population to decline.

Not surprisingly, the truth in any given predator-prey system often lies somewhere between with some predation being compensatory and some being additive. The trick is to determine degree. If predation has an “additive,” or negative, effect on prey population growth, is the effect small or large?

Jacques and Van Deelen applied statistical analysis to ten years of field and registration data (1998-2008) supplied by hunters from 57 deer management units, or DMUs, in the northern and central forests.

This 10 year period coincides with a steady increase in wolf populations and a probable increase in bear populations in the northern and central forests.

The Wisconsin researchers were looking for relationships, or correlations, within this large mass of data. For instance, do the data show a relationship between increasing wolf numbers in a given area and the growth rate of the deer herd? If such a relationship is revealed, researchers call this a “signal.” The signal can be positive or negative, weak or strong.

This statistical analysis does not show cause and effect, Van Deelen cautions. Nevertheless, the numerical “signals” it produces are valuable markers, pointing to areas where further research is needed to explain the numbers.

The statistical model created by Jacques and Van Deelen suggests black bear presence is associated with a reduced population growth rate for deer of less than one percent. Under this model deer herds would still grow in the presence of a large bear population, just at a

slightly reduced rate. The model also suggests that the presence of wolves is related to a slightly increased rate of doe mortality.

“This early analysis appears to say that impacts on deer populations associated with bears and wolves are clearly minor relative to impacts associated with hunting by humans,” said Van Deelen.

These statistical relationships reflect what could be happening across large regions according to biologists. The numbers have nothing to say when it comes to an individual hunter and the 40 or 80 acres he or she hunts.

“If you happen to be hunting in an area of wolf activity,” Jacques said, “it could affect deer behavior or movement patterns and the number of deer you see.”

DNR wildlife officials are committed to continually improving the quality of the state’s deer management program. Hunters play a critical role in this process, and as the agency moves forward with its ambitious research program, hunter involvement will be more important than ever.

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Impacts of predators on white-tailed deer population growth and recruitment in Wisconsin

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Introduction

Estimating the number of white-tailed deer (*Odocoileus virginianus*) in Wisconsin has been controversial for many years. In 1943 Aldo Leopold estimated the Wisconsin deer population at 500,000 animals. His estimate was questioned by Roy Jorgensen, editor of “*Save Wisconsin’s Deer*” who instead suggested there were 200,000 deer. Despite uncertainty in population estimates, Wisconsin is considered one of the premiere deer hunting states in the United States. Annual gun harvest by Wisconsin deer hunters have increased from an average of 90,000 from 1961-1969 to more than 383,000 from 1990-1995. More recently, the annual gun harvest by Wisconsin deer hunters has increased to an average of 471,000 from 1996-2007. Importantly, overabundant deer populations during these time periods are likely associated with widespread baiting and feeding practices, mild winters, and inadequate harvest throughout much of the state. Consequently, deer overabundance issues have established an unfortunate precedent and unrealistic harvest expectations by Wisconsin deer hunters. Despite record deer harvests during this time period, reduced deer harvests occurred during the 2008 and 2009 firearm seasons. Though reduced harvests were likely associated, in part, with regional variation in environmental factors (i.e., abundance of standing corn, below average ambient temperatures, presence of dense fog, etc.) and widespread use of harvest regulations (Earn-A-Buck) across much of Wisconsin, increased concern about potential impacts of predation on deer population growth and recruitment also has been suggested by a diverse group of stakeholders interested in Wisconsin’s deer management program as a factor contributing to perceived deer population declines during the past 2 years. Though uncertain, it is possible that increasing predator populations across Wisconsin during the past 20-25 years has contributed to notable increases in predation rates, and potential additive effects on annual mortality and subsequent deer population growth and recruitment. Thus, this project was undertaken in response to legislative and stakeholder demands for an evaluation of potential predation impacts on Wisconsin deer populations. Our specific goals were to conduct a comprehensive review of the existing ecological literature relative to predation on white-tailed deer, and to theoretically estimate potential bear and wolf effects on deer population growth and recruitment across northern and central Wisconsin.

Effects of predation on white-tailed deer populations are difficult to measure and generalities are difficult to identify because effects of predation can vary with ecological context (Gasaway et al. 1983, Messier 1991, Patterson and Power 2002). Nonetheless, most consumptive users of deer concluded long ago that every deer killed by a predator was wasted and resulted in one less deer available for a hunter to harvest (Mech 1984). Such widespread perception was part of the public’s general attitude that predators were significant competitors with humans—an attitude that continues to persist today (Mech 1984, Meadow et al. 2005). However, our understanding about predation impacts on deer population dynamics is still being evaluated by wildlife biologists and researchers,

for predator-prey interactions are both spatially and temporally variable. There is little reason to believe that relationships that characterize one predator-prey system are applicable for all systems (Mech 1970), or even for the same system under different conditions (Mech 1966).

White-tailed deer are preyed upon by a wide variety of predators—a situation easily discerned from many predator species' characteristics (Mech 1984). For instance, the broad geographic distribution of deer facilitates increased contact with both northern and southern carnivores. In the northern part of its range (northern United States and Canada) deer regularly contend with snow and low ambient temperatures, thereby adding significantly to their vulnerability to annual mortality events (Mech 1984). Restricted mobility in deep snow, reduced food intake, increased exposure to cold each winter may contribute directly to deer mortality, or, under less extreme environmental conditions, greatly predispose them to predation events (Mech 1984). Thus, it is little surprise that under some conditions nearly every type of carnivore that occurs sympatric with deer will feed on deer, including coyotes (*Canis latrans*), foxes (*Vulpes vulpes*), domestic dogs (*Canis familiaris*), bobcats (*Lynx rufus*), black bears (*Ursus americanus*), mountain lions (*Puma concolor*), wolves (*Canis lupus*), wolverines (*Gulo gulo*), golden eagles (*Aquila chrysaetos*), bald eagles (*Haliaeetus leucocephalus*), fisher (*Martes pennanti*), and lynx (*Lynx canadensis*). However, the relative impact of predators on deer population dynamics is variable. In Wisconsin, only wolves, coyotes, black bears, and bobcats conceivably could kill enough deer to negatively impact deer populations to any significant degree. However, no studies in the Great Lakes region or elsewhere in North America have found fishers to be a significant predator on white-tailed deer.

Wolves and Bears

Prior to 1900, gray wolves (*Canis lupus*) ranged over most of North America. However by 1950, wolf populations were extirpated from the continental United States except for Alaska and northeastern Minnesota (Ballard and Gipson 2000). By about 1975, dispersing wolves began recolonizing their former range in northern Wisconsin (Thiel 2001). Early population growth was slow and wolves numbered ≤ 40 individuals until the early 1990s when the Wisconsin wolf population entered a period of sustained growth (Wydeven et al. 2009a). Growth of the wolf population in Wisconsin was facilitated by regulatory protection under State and Federal Endangered Species laws and, likely, by burgeoning growth in northern Wisconsin's white-tailed deer population that occurred coincident with wolf recovery (Wydeven et al. 2009a, Wisconsin Department of Natural Resources 2001). Today, approximately 626–664 wolves exist throughout northern and central Wisconsin (Wydeven et al. 2009a).

Diets of wolves vary by location and by month, season, or year and are influenced, in part, by abundance of specific prey (Thompson 1952; Theberge et al. 1978; Fritts and Mech 1981; Fuller 1989). Before wolves were extirpated in Wisconsin, white-tailed deer occurred in >90% of scats annually (Thompson 1952). In early re-colonizing wolves in Wisconsin, about 55% of scat volume was deer, but samples were biased toward warmer

months (Mandernack 1983); by all measures deer were the major prey of wolves during winter and summer.

Our understanding of the components of population performance of deer was limited through the mid-1900s and concurrent with the extirpation of wolves from Wisconsin, Michigan, and much of Minnesota. Prior to the use of radio-collars in the 1960s our knowledge of how long deer lived, and when and why they died, was incomplete. An accurate technique for aging deer by evaluating their teeth (Gilbert 1966) enabled researchers to show that wolves in northeastern Minnesota killed disproportionately more fawns and older deer compared to deer killed by hunters (Erickson et al. 1961; Mech and Frenzel 1971). On average, deer killed by wolves and hunters were 4.7 and 2.6 years old, respectively. These age-specific impacts on deer were later confirmed relative to the recovering population of wolves in northcentral Minnesota (DelGiudice et al. 2002, 2006).

Before the recovery of wolves in Wisconsin, deer populations were likely limited by recreational hunting, winter mortality, and density-dependant interactions with food resources. However, the extent to which wolf predation is an additive limit on growth of deer populations is unknown (Van Deelen et al., unpublished data). The impact of a new source of mortality (increasing bears, recovering wolves) can be obscured by compensatory responses from other sources of mortality (car kills, hunting, severe winters, etc.) and from increased reproduction. Thus, the best measure of the effects of a new mortality source on a population would be changes in the population's growth rate because the growth rate integrates the various mortality rates, reproductive rate, and all of their interactions (Sibley and Hone 2003).

Importantly, previous research indicates that deer populations would normally need to be reduced to fewer than 3 deer/mi² for wolves to limit deer population growth (Mech 1984). Wolf predation is not generally a major mortality factor until deer densities decline below 10 deer/mi² (Wydeven 1995). Deer densities of fewer than 10 deer/mi² occur infrequently in Wisconsin. Wolves in the Great Lakes Region normally consume 15–19 adult-sized deer (or their equivalent) per wolf per year (Fuller 1995, Mech and Peterson 2003). At a rate of 19 deer per wolf pack per year, an average Wisconsin wolf pack of four wolves on a 70 mi² territory would consume approximately 76 deer or ~1 deer per square mile. Thus, Wisconsin's wolf population during late winter 2009, which consisted of 626–662 wolves, may have consumed between 9,390 and 12,578 deer. Importantly, the total 2008 deer harvest within the central and northern forest zones where wolves occur sympatric with deer was 122,000 (gun and archery). Additionally, approximately 13,000 deer were killed in these zones by motor vehicles during 2008.

Prior to 1985, unlimited and increasing harvests caused Wisconsin's black bear population to rapidly decline. Following a close of the bear season in 1985, and with the cooperation of major hunting organizations and the passage of authorizing legislation, a new system of bear hunting and harvest control began in 1986. Since then, evidence suggests that the bear population estimate in Wisconsin has more than quadrupled from a

low of <6000 in 1985 to 26,000–40,000 in 2007–2008, and concurrent with an expanding statewide deer population since the mid-1980s.

Previous research from across the United States has documented bear predation rates on radiocollared deer fawns of 10–57% (Table 1), but few studies have determined how important such predation is on deer population growth. In most studies where black bears occur sympatric with deer, predation by bears is limited to fawns <45 days old (Franzmann et al. 1980, Ballard et al. 1981, Ozoga and Verme 1982, Smith 1983, Mathews and Porter 1988, Vreeland et al. 2004); most predation occurs in the first 2 weeks after fawns are born. Kunkel and Mech (1994) reported that during their study, bears did not appear to actively hunt fawns. Rather, they detected fawns up to 10 m away incidentally while feeding on insects and vegetation and rushed them once detected. Because newborn deer fawns are only seasonally available (Rutberg 1987), year-round predation by black bears is impossible. Importantly, bear populations in northern Wisconsin have been relatively high for at least 10 years (Rolley and Worland 2009a), despite perceptions of a sudden dramatic increase in bears and an associated increase in fawn predation. Consequently, bear predation on fawns has been occurring for decades and clearly not a recent phenomenon.

Modeling wolf and bear impact on deer population growth and recruitment

The Wisconsin DNR has worked cooperatively with the University of Wisconsin-Madison on a preliminary and exploratory/correlational joint analysis of impacts of human hunting and predation by wolves and black bears on population dynamics of deer in northern Wisconsin. The backbone of this analysis is a mixed effects regression model with a repeated measures design. This analysis was conducted for 57 northern and central forest deer management units (DMUs) over a 10-year period (1998–2008). Consequently, this time period corresponds to an increase in Wisconsin's wolf population from a minimum of 178 wolves in 1998 (Wydeven et al. 2009a) to a minimum of 520 in 2008 (Wydeven et al. 2009b) and a bear population that has been slowly increasing since the early 1990s (Rolley and Worland 2009b). It should be noted that our analysis is exploratory and attempts to describe correlational relationships between deer population growth and recruitment as impacted by predators. Thus, limitations apply here because our BEAR HABITAT variable was an indirect way of estimating bear effects, and was used because we had access to neither DMU-level measures of bear population density nor actual predation by bears. Further, our WOLF variable was used because once again, we did not have access to actual predation by wolves.

Nonetheless, the dependent variables in our analysis included DMU-level estimates of population growth rate and recruitment. The growth rate was calculated as

$$r_{DMU} = \ln \left(\frac{N_t}{N_{t+1}} \right),$$

where N is the DMU-level population estimate for time t . The DMU-level measures of recruitment were 1) the proportion of fawns in sample of antlerless deer aged during fall harvest ($pFAWNS$) and 2) the proportion of yearling females ($pYRFEM$) in the sample of yearling and older females aged during the fall harvest. Predictor variables included year

(*YEAR*), DMU-level estimates of prehunt deer density from the WDNRs Sex-Age-Kill (SAK) model (*DDENS*), deer harvested/km² deer range (*HARV*), wolves (*WOLF*), and bears (*BEAR HABITAT*). We calculated the *WOLF* variable as the percentage of the DMU overlapped by known wolf pack territories for year *t*. We constructed the *BEAR HABITAT* variable from DMU-level estimates of bear occupancy (calculated from habitat features, MacFarland 2009) and yearly DMU-level black bear harvests (an indication of black bear presence). Unfortunately, the level of detailed data used for our wolf analysis was not available for bears. Consequently, we lacked DMU- and year-specific information on changes in bear distribution and abundance. Thus, the best information available for our bear analysis was geographic differences in bear habitat suitability. Measures of direct occupancy were unavailable, thus habitat suitability was derived from available habitat occupancy data. The distribution of black bear harvests across all years and all DMUs had a 5th percentile of 5 bears. We used this variable as a threshold value to separate DMUs with healthy bear populations from those with marginal, transient, or absent bear populations. Thus, *BEAR HABITAT* was assigned a value of 0 for combinations of year and DMU where bear harvest was <5 bears, otherwise the value of *BEAR* was the calculated probability of occupancy (MacFarland 2009).

The repeated measures design was implemented to account for the fact that all variables are repeatedly measured at the level of the DMU for each of 10 years (1998-2008, Littell et al. 2006, Van Deelen et al., unpublished data). We included DMU as a random effect to account for unmeasured effects that are characteristic of different DMUs. Fixed effects were *YEAR*, *DDENS*, *HARV*, *WOLF*, and *BEAR HABITAT*, and the interaction terms for the hunter/predator effects: *HARV*WOLF*, *HARV*BEAR HABITAT*, and *WOLF*BEAR HABITAT*. Variables were transformed as needed to meet the assumption of normality. Interpretation of the interaction terms is useful for inferring the extent to which hunting mortality and predator effects are compensatory or synergistic.

Model diagnostics suggested that the repeated measures design was a reasonable way of analyzing the data. Significant effects (Type 3 test of fixed effects, PROC MIXED, SAS 9.22; $P < 0.05$) in the analysis of growth rates were *YEAR*, *DDENS*, *HARV*, *BEAR HABITAT*, and *HARV*BEAR HABITAT*. Parameter estimates suggested that growth increased with increasing density but decreased with increasing harvest, and increasing bear effects. The parameter for the interaction term (*HARV*BEAR*) was small but positive, indicating some compensatory interaction between hunter harvests and bear effects. Our findings of increasing growth as a function of increasing deer density (inverse density dependence) is not intuitively obvious and may be associated with variable carrying capacities across deer management units and relatively less variation in hunter harvest with respect to DMU-specific deer densities and carrying capacities. However, this hypothesis is weakly supported by empirical data and clearly requires further investigation.

Significant effects in the analysis of *pFAWN* were *YEAR*, and *DDENS* ($P < 0.05$). *BEAR HABITAT* and *HARV*BEAR HABITAT* were marginally significant ($P = 0.07$ and $P = 0.06$, respectively). Parameter estimates suggested that the percent of fawns in the samples of antlerless deer aged at harvest decreased with increasing prehunt deer density.

Percentage of fawns tended to be lower in deer management units with more suitable bear habitat (though significance was marginal, $P = 0.07$). Further, increasing harvest also was negatively related (though not significantly $P = 0.37$) to increasing bear effects. Again, the parameter for the interaction term was positive, indicating some compensation between hunter harvest and bear effects. Admittedly, these relationships also may be associated with varying hunter densities or bear habitat suitability across the north (lower hunter densities and higher bear habitat suitability in the northwest than northeast), or lower fawn:doe ratios in northwestern Wisconsin. However, these hypotheses are currently unsupported by empirical data. Significant effects in the analysis of *pYRFEM* were *YEAR* and *DDENS* ($P < 0.05$). Bear effects were marginally significant ($P = 0.06$). Parameter estimates for *DDENS* and *BEAR HABITAT* were negative, suggesting that percent of yearling females among yearling and adult females in the harvest declined with increasing prehunt density and bear effects.

Presence of *YEAR* as a significant effect in each of the 3 analyses suggests that the dynamics of deer in northern Wisconsin experienced significant variation in response to yearly differences from 1998–2008. The mechanisms contributing to these differences are not clear but weather is known to impact both recruitment and survival of northern deer (Patterson and Power 2002), thus it's reasonable to assume that weather is a component of the year effect we measured. Each analysis included a significant effect for deer density (*DDENS*). In the case of recruitment (*pFAWN* and *pYRFEM*), the relationship was negative as would be associated with density dependence acting to progressively restrict recruitment as density approached carrying capacity (McCullough 1979). The positive relationship between deer density and population growth may be spurious because density is used to calculate growth, thus density appears on both sides of the equation. Alternatively, density and growth may share an association with habitat such that high density and high growth rates occur together in DMUs with highly productive habitat while the opposite is true for DMUs with less productive habitat. Admittedly, this relationship is counter intuitive and warrants additional investigation.

Hunting: Increasing harvest intensity had a predictably negative relationship to population growth rates. This is reassuring since regulation of harvest is used by DNR to manage the growth rates of Wisconsin deer herds. Harvest was not a significant effect in the 2 analyses of recruitment except as part of the interaction term (*HARV*BEAR HABITAT*) in the analysis of fawn proportions in the harvest. This probably relates to the fact that deer hunters are relatively non-selective in the harvest of antlerless deer and that changes in intensity of antlerless harvests impact fawn, yearling and adult cohorts relatively equally.

Bears: Bear habitat effects were significantly, or nearly so, negatively associated with population growth and with the proportion of fawns and yearlings in the antlerless harvest consistent with a hypothesis that black bear predation acts as a limit to the growth of deer populations through predation on fawns. However, our findings suggest correlational relationships between areas of higher bear habitat suitability and areas of lower deer population growth and fawn production/yearling recruitment. Because bear harvest rates likely vary across regionally across Wisconsin, it remains unknown whether

bear population density is directly related to habitat suitability. Recent literature suggests that bears are efficient predators on fawns but not older deer (Vreeland et al. 2004). As we measured it, the growth rate model predicts that the bear effect by itself would equate to a 10-18% reduction in DMU-level growth rates over the range of bear habitat suitability (or at least modeled occupancy) values in Wisconsin DMUs. Similarly the fawn percentage model predicts a 1-2% decrease in the percentage of fawns comprising the annual harvest. Once again, caveats apply here because our BEAR HABITAT variable is a very indirect way of estimating bear effects, and was used because DMU-level measures of bear population density and predation by bears have not previously been quantified in Wisconsin, hence could not be incorporated into our analysis. Also, both models included a compensatory term (HARV*BEAR HABITAT) that, on average, would mitigate deer population growth by approximately 5–9% and the fawn percentage by 3–4%. In the case of *pFAWN*, the compensatory effects essentially cancel the *BEAR HABITAT* effects. Our findings of a potential bear effect on fawn mortality (1–2%) are lower than preliminary findings from ongoing research in the Upper Peninsula of Michigan on deer fawn survival, where researchers documented that approximately 4% of mortalities were attributed to black bear predation (Duquette et al. 2010). However, our findings are based largely on correlational (theoretical) analyses rather than field based research, thus, should be interpreted with caution.

Wolves: Wolf effects were virtually nonexistent. Percent overlap of DMUs by known wolf pack territories ranged from 0 to 91%, however tests for significance of *WOLF* and interaction terms containing *WOLF* indicated no effect ($0.12 < P < 0.86$) on deer population growth rates and fawn survival.

Overall it does not appear that wolves are likely to be a major mortality factor on deer population growth in northern and central Wisconsin under current conditions or in the near future (Schultz et al. 1999). Even with a population of approximately 650 wolves, annual predation of 11,700 deer would represent only 0.3% of the overwinter population goal of 348,000 deer in the northern and central forest regions. Additionally, the average fall deer population for the area exceeds 450,000. A large proportion of northern Wisconsin deer die from natural causes, which can vary dramatically depending on severity of winter (Creed et al. 1984). Wolves would probably remove some of these animals that would die from other causes. A deer killed by wolves would not be killed by winter stress or other mortality sources. Consequently, much of the mortality by wolves would likely compensate for other natural mortality because it occurs year-round (Schultz et al. 1999).

Conclusion: We emphasize that our analysis is both preliminary and based largely (if not entirely) on an exploratory and correlational approach. The dependant variables are indirect estimates of the actual phenomena that they presumably represent. Growth rates are calculated from SAK estimates that are known to include large and unpredictable variations (Millspaugh et al 2009). That said, both growth rate and recruitment are characterized by substantial yearly variation apart from variation in density and harvest at the DMU level. Increasing harvests associate with reduced growth and recruitment as expected and recruitment appears to be density-dependant. Bears appear to affect both

growth and recruitment and although our analysis is consistent with predation as a mechanism we are unable rule out other mechanisms such as a negative association with the same habitat features that predict bear occupancy. Further, wolf effects, measured as the physical presence of a wolf pack territory in DMUs, had no discernable impact on population growth rates or recruitment of deer in Wisconsin. Correlational relationships identified during our analysis are suggestive of several research hypotheses regarding impacts and relative magnitude of predator effects on fawn survival and subsequent recruitment across northern and central Wisconsin. Clearly, these hypotheses warrant further investigation through field-based research.

Coyotes

Though estimates of coyote population abundance in Wisconsin are unknown, annual harvest data suggests a significant (123%) upward trend in coyote population abundance since the mid-1990s (Dhuey 1996, 2009). Additionally, trend data indicate that coyote sightings vary regionally across Wisconsin. For instance, coyote sightings have increased 3-to-5 fold in all but the northern forest region between 1998 and 2008. In the northern forest region, sightings remained relatively stable from 1988-1998, and have slowly increased since 2000 (Kitchell 2009).

In most forested areas of northeastern North America, white-tailed deer are a primary prey species of eastern coyotes (Messier et al. 1986, Parker 1986, Patterson et al. 1998). Many studies have assessed fawn mortality throughout North America (Huegel et al. 1985, Nelson and Woolf 1987, Decker et al. 1992, Long et al. 1998, Ballard et al. 1999). However, relative to the extensive geographic range of deer, distribution of fawn mortality studies is limited. Fawn mortality studies elsewhere have identified predation, legal and illegal harvest, disease, starvation, malnutrition, parasites, accidents, collisions with vehicles and farm machinery, and other causes of mortality (Vreeland et al. 2004).

Where coyotes and deer occur sympatric, it is likely that some level of predation on fawns occurs; however, previous research has shown the extent and timing of predation varies both spatially and temporally within an area (Nelson and Woolf 1987). Because newborn fawns are only seasonally available, it is impossible for coyotes to be a year-round fawn specialist. Nonetheless, estimates of the percent of mortalities attributed to coyote predation are well documented in the ecological literature, ranging from 0 to nearly 100% (Table 1). Despite high variability in the percent of mortalities caused by coyotes, information on seasonal and annual predation rates (defined as the percentage of animals preyed on) is particularly meaningful to game managers tasked with managing deer populations. Fortunately, seasonal and annual coyote predation rates are well-documented across eastern North America, particularly for fawns. In Pennsylvania, coyote predation (17%) was the leading cause of fawn mortality in extensively forested areas (Vreeland et al. 2004). In other forested regions, Long et al. (1998) and Ballard et al. (1999) attributed 28% and 18% of fawn mortalities to coyotes, respectively (Table 1). Across Michigan, Illinois, Iowa, Colorado, Texas, Oregon, and Oklahoma, percentage of fawns killed by coyotes range from 1–69% (Table 1). In Minnesota, Schulz (1982) documented no predation and Bryan (1980) estimated only 2% loss due to coyote

predation in central Missouri. In an intensively farmed region of southern Minnesota, Brinkman et al. (2004) reported that 5% of 39 captured fawns were killed by coyotes. In an exurban area of Alabama, Saalfeld and Ditchkoff (2007) attributed 28% of 36 fawn mortalities to coyotes and concluded that coyote predation was the leading cause of fawn predation during their study. They speculated that observed fawn predation rates may have been a function of sampling biases of other regional studies, sparse bedding cover, and late birthing seasons typical of southern, exurban deer populations. The timing of the fawning season in Alabama is later than in other deer populations and occurs from late July to early September (Gray et al. 2002), which coincides with the greatest hunting population of coyotes because pre-dispersal coyote pups are hunting independently at this time (Harrison and Harrison 1984, Harrison et al. 1991). Elsewhere in the southeastern United States, Kilgo et al. (unpublished data) presented circumstantial evidence from South Carolina and Alabama suggesting that coyotes may be impacting deer recruitment. Specifically, they presented 5 pieces of evidence consistent with a potential coyote effect on deer recruitment. First, the statewide deer population in South Carolina has declined coincident with the establishment and increase in the coyote population. Second, datasets from the Savannah River Site (SRS) in South Carolina indicate a new mortality source impacting the deer population coincidental with the increase in coyotes. Third, an index of deer recruitment at SRS declined coincident with the increase in coyotes. Fourth, food habits data from SRS indicate that fawns are an important food item for coyotes during summer. Finally, recent research from Alabama documented significant coyote predation on fawns there. Although this evidence does not establish cause and effect between coyotes and observed declines in deer recruitment, the authors argue that additional research should proactively address this topic in the region.

Similarly, VanGilder et al. (unpublished data) investigated impacts of predators on deer recruitment, and inferred predation impacts by comparing fawn to doe (FDR) ratios before and after an intensive predator removal on an 800-hectare study site in northeast Alabama. Fawn-to-doe ratios were estimated prior to intensive removal of predators (22 coyotes, 10 bobcats) during February–July 2007. Consequently, the September (pre-hunt) FDR increased from 0.18 to 0.24 and the February (post-hunt) FDR increased from 0.41 to 1.20 in the years following predator removal. Thus, the authors concluded that predation on fawns may reduce recruitment in some areas of the Southeast, and that intensive predator removal prior to the fawning season may be effective at increasing recruitment in some areas where herd productivity does not meet management objectives.

In contrast, Pusateri Burroughs et al. (2006) documented virtually no coyote predation on fawns (Table 1), hypothesizing that low coyote mortality in southwestern Lower Michigan may have been associated with an abundance of alternate food sources that sustained local coyote populations. Alternatively, they suggested that coyote densities may have been lower than previously documented, or that dense ground cover may have provided fawns with additional protection from predation events.

In a recent fawn survival study in southern Illinois, coyotes were identified as the most prominent predator, accounting for 56% of all predation and causing 79% of predation when it was possible to identify the predator species (Rohm et al. 2007). Despite a high

percentage of mortalities attributed to coyote predation, only 13.9% of 166 fawns captured during this study were killed by coyotes (Rohm et al. 2007). Following the first of 3 field seasons in a study evaluating the role of predators, winter weather, and habitat condition on white-tailed deer fawn survival in the south-central Upper Peninsula of Michigan, researchers documented that 39% of 48 fawns were killed by predators within 4 months post-capture, of which 15% were killed by coyotes (Duquette et al. 2010). The majority of mortalities occurred during two periods, from late-May through mid-June and from late-July through mid-August. These findings suggest that predation may be an important factor influencing fawn survival in subsequent years of this study.

High variability in reported predation rates is associated with many intrinsic and extrinsic factors (Porath 1980, Linnell et al. 1995), most notably heterogeneity in landscape and habitat characteristics. For instance, Carroll and Brown (1977) noted reduced coyote predation rates in years with increased availability of hiding cover for fawns. While studying fawn survival in southern Illinois, Nelson and Woolf (1987) found that coyote-killed fawns tended to occupy home ranges in open habitat and fields. Moreover, Rohm et al. (2007) suggested that because coyotes were the primary predator during their study, habitat characteristics associated with fawn survival areas may have represented landscapes where coyotes were less effective at locating and killing fawns. Several studies have shown that coyotes prefer more open habitats as opposed to forested habitats (Priest 1986, Cypher 1991, Person and Hirth 1991, Holzman et al. 1992). Consequently, Rohm et al. (2007) hypothesized that this may have contributed to higher fawn survival in areas with few large forest patches adjacent to smaller patches of other cover during their study. Gehring and Swihart (2003) observed coyotes avoiding forest patches during summer months, further suggesting that forest patches may provide cover for fawns during a time of increased vulnerability to coyote predation. Furthermore, there is evidence that coyotes are less efficient foragers in forested landscapes compared to more open areas (Gese et al. 1996, Richer et al. 2002). If coyotes are less efficient foragers in forested landscapes or patches, this provides further support that fawns seeking cover in large forested areas would be less vulnerable to coyote predation than fawns inhabiting relatively more open habitats, other cover types, or smaller forest patches (Rohm et al. 2007). Consequently, ecological landscapes throughout Wisconsin vary along a latitudinal gradient from north to south, thus, importance of predation impacts on deer populations also (presumably) vary along this gradient. For instance, variable land use practices and predator densities clearly vary along a latitudinal gradient, with greater agricultural practices and coyote densities in the farmland deer management regions than in the northern forest region. Thus, impacts of coyote predation on deer survival likely vary between northern and southern Wisconsin. However, previous research evaluating impacts of predators on fawn survival and subsequent recruitment has not previously been documented in Wisconsin.

Ability or willingness of coyotes to exploit fawns may be explained by optimal foraging theory (MacArthur and Pianka 1966, Stephens and Krebs 1986, Rohm et al. 2007) and a coyote's ability to switch prey items. Coyotes have a diverse diet that changes throughout the year, depending on prey availability (Andelt et al. 1987, Windberg and Mitchell 1990), and they can switch from preying on small mammals (i.e., their primary

prey) to preying on deer fawns (Hamlin et al. 1984, Patterson et al. 1998). Smith (1984) noted considerable variation in occurrence of white-tailed deer in coyote scats in northern Wisconsin, with a notable increase in percent occurrence of fawn remains in scats between early May (pre-fawning; 39%) to late June (fawning; 60%). Further, Niebauer (1974) also noted considerable prey switching by coyotes in northwestern Wisconsin, with the highest occurrence of deer in coyote scats in June, which coincided with peak fawning in northern Wisconsin. Given the vulnerability and size of young fawns relative to small mammals, it would be beneficial for coyotes to capture fawns as long as searching for and subduing fawns does not exceed the benefit derived from consuming them. Harrison and Harrison (1984) found that breeding coyotes and their pups had higher occurrences of fawn remains than small mammals in coyote scats. Consequently, they hypothesized that this may have been due to fawns being energetically or nutritionally more efficient for coyotes to prey upon than catching small mammals. Regional trends in percentages of yearling female deer comprising the annual gun harvest across Wisconsin suggest that variation in landscapes may influence coyote predation rates on deer fawns. For instance, percentage of yearling female deer harvested across the northern forest region has averaged 27% during the past 40 years (Wisconsin Department of Natural Resources, unpublished data) with no sustained downward trend since the late 1990s that would correspond to increasing predator populations and subsequent predation rates on fawns. However, percentage of yearling females harvested across the southern farmland region has declined from 49% during the mid-1980s to 29% in 2009 (Wisconsin Department of Natural Resources, unpublished data) and corresponds to expanding coyote populations throughout the region. Given the ability of coyotes to switch prey and optimal foraging theory, notable differences in yearling recruitment indices across Wisconsin may be influenced, in part, by variation in predation rates on fawns as influenced by differences in landscape characteristics between northern and southern Wisconsin. Though uncertain, it is possible that densely vegetated landscapes throughout the northern forest region may hamper coyote search efforts, thereby diminishing the benefits of capturing fawns (as reflected in variable yearling doe harvests). However, in more open habitats typical of the farmland regions of Wisconsin, it may be beneficial for coyotes to switch from their primary prey (small mammals) to fawns (as reflected in the long-term declining trend in yearling doe harvest).

Additionally, adult deer mortality attributed to coyote predation is well-documented in the ecological literature and can be a major source of mortality for deer along the northern extent of their geographic range in North America. If coyotes primarily remove deer that would have died of other causes in the absence of predation (i.e., compensatory mortality), predator impacts would be minimal regardless of the number of deer removed (Patterson and Messier 2003). However, coyote predation can be a significant source of mortality for adult deer (Whitlaw et al. 1998, Patterson et al. 2002), particularly during severe winters. Thus, additive effects of coyote predation on deer populations also must be considered. For instance, Lavigne (1992) determined that 50–70% of the deer in a sample of 863 deer killed by coyotes in Maine were in good physical condition. Because nearly half of those deer were classified as adults, Lavigne (1992) suggested that coyote predation may have been additive to mortality due to other factors. Messier et al. (1986) and Brundige (1993) also reported that the physical condition of deer killed by coyotes

was as good or better than that of the general deer population. Patterson and Messier (2003) reported that coyotes preyed largely upon prime-aged (adult) deer in apparently good physical condition. Though manipulative experiments are needed to definitively demonstrate additive mortality, Patterson and Messier (2003) concluded that coyote predation was largely additive to mortality due to other factors during their study. Whitlaw et al. (1998) reported that most (64%) adult female deer mortalities in northern New Brunswick were attributed to coyote predation, and occurred during winter when deer were likely more vulnerable to coyote predation than during spring or summer months. Despite a high percentage of mortalities attributed to predation, regional predation rates (i.e., percentage of animals killed by predators) varied between 11 and 33% (Whitlaw et al. 1998; Table 1). Nevertheless, coyotes were the most significant predator of adult deer in New Brunswick and southern Quebec (Whitlaw et al. 1998). During their investigation of factors contributing to a declining deer population in Nova Scotia, Patterson et al. (2002) documented a moderate predation rate (24%; Table 1) and concluded that coyote predation (combined with unregistered harvest of adult female deer) likely contributed to slowed regional deer population growth rates. Parker (1995) estimated that coyotes in New Brunswick probably kill 2 or more deer per year per coyote, which may or may not reflect coyote predation rates on adult deer elsewhere. Interestingly, recently published research hypothesized that coyote predation on adult deer in southeastern Canada and northeastern United States may have been greater than other portions of coyote range because coyotes in these regions are larger and have apparently bred with eastern wolves (*Canis lycaon*) in the past (Kays et al. 2010, Way et al. 2010). However, it remains uncertain whether body size impacts coyote predation rates on adult deer throughout other regions, particularly the Great Lakes Region. Evaluating potential effects of coyote body size on subsequent deer predation rates through field based research is needed to better understand predation effects on deer population growth and recruitment throughout Wisconsin.

Conclusion: Despite high variability in reported predation rates across the geographic range of deer, no studies have asserted that coyote predation suppresses deer population growth for extended time periods. Though coyote density may not be high enough in a particular area to suppress long-term deer population growth, when added to non-compensatory mortality caused by other sources of mortality, coyote predation could have a significant impact on deer populations. Future research evaluating survival and cause-specific mortality of adult deer may help to elucidate potential impacts of coyotes on deer population growth throughout Wisconsin. Further, research investigating spatial distribution of coyotes relative to established wolf packs may provide insight into how wolves may be limiting coyote populations where the two species occur sympatric with deer populations, thereby minimizing coyote impacts on deer survival (particularly fawns) and yearling recruitment across northern and central Wisconsin. However, these hypotheses are currently unsupported by empirical data and require field based research to better understand spatial and temporal distribution patterns of these predators, and subsequent impacts on deer population growth and recruitment in Wisconsin.

Bobcats

Bobcats are the most generalist of all the North American felids and is the felid most involved in predation on deer fawns (Linnell et al. 1995). Vreeland et al. (2004) reported that bobcats were responsible for 3 of 106 (3%) fawn mortalities within 34 weeks of capture in Pennsylvania, of which 6% of fawns killed by predators were attributed to bobcat predation (Table 1). Elsewhere, bobcats predation was documented in Massachusetts (Decker et al. 1992), New Brunswick (Ballard et al. 1999), Texas (Cook et al. 1971), Oklahoma (Bartush and Lewis 1981), and South Carolina (Epstein et al. 1983, 1985), however, predation rates were low overall in these studies ($\leq 7\%$) and were not thought to limit population growth or recruitment rates in local deer populations. Preliminary results from the fawn survival study in the south-central Upper Peninsula of Michigan, researchers documented that bobcats killed 10% of 48 fawns within 4 months post-capture (Duquette et al. 2010). These findings are similar to reported bobcat predation rates (9.5%) documented in an endangered Columbian white-tailed deer population in western Oregon (Ricca et al. 2002). In contrast, Carstensen et al. (2009) reported that bobcats accounted for 8 of 17 deaths of deer fawns during one summer in Minnesota; bobcat predation accounted for the majority of fawn mortality during their study and overall summer survival (12 weeks post-capture) of fawns (0.47) was slightly less than 50% in this study. Importantly, these findings suggest that bobcats could have a significant impact on deer survival (particularly fawns) throughout the Great Lakes Region, and elsewhere.

The consensus of wildlife managers and researchers studying bobcat predation on deer is that such predation usually is compensatory to a variety of other mortality factors (i.e., winter severity, starvation, disease, other predators etc.) and likely not intensive enough to negatively affect deer abundance (Hosley 1956, Connolly 1978). Because bobcats prey mainly on rabbits, hares, squirrels, porcupines, and other small mammals and birds, they rarely affect deer populations significantly (Marston 1942, Mech 1984). Analyses of harvest data suggest that the fall bobcat population in northern Wisconsin fluctuated between 1,500–1,800 during the 1980 and early 1990s, and increased to a high of approximately 3,100 animals in the early 2000s (Rolley and Worland 2009). Subsequent bobcat populations have stabilized and declined to approximately 2,100 animals in recent years across northern Wisconsin. Because Wisconsin's bobcat population is small relative to the deer population, impacts of bobcat predation on deer population growth and recruitment are likely minimal. However, when effects of bobcat predation are added to other non-compensatory mortality factors, bobcats could have a significant impact on deer population dynamics, particularly fawn survival and recruitment. To better understand potential impacts of bobcats on deer population growth and recruitment in Wisconsin, direct measures of bobcat predation through field-based research are needed.

Some final thoughts

Several studies have shown that ungulates exhibit a behavioral effect in the presence of wolves by increasing their vigilance, or altering their space use and travel patterns to avoid wolves (Hebblewhite et al 2002, Ripple and Beschta 2004, Nelson and Mech 2006, Proffitt et al 2009). Indeed Rooney and Anderson (2009) reviewed potential for wolf-initiated trophic cascades in the Great Lakes region and argued that increasing deer populations have occurred concurrently with increasing wolf numbers, thereby suggesting a minimal numerical response of deer population growth to wolf predation. An alternative mechanism for reduced deer densities in the presence of wolves may have been more associated with behavioral responses (increased predator avoidance strategies including increased vigilance or spatial/temporal use of habitat inaccessible to hunters), which consequently exaggerate hunter perceptions of deer population declines (Van Deelen and Etter 2003).

Though impacts of predators on deer population growth and recruitment vary considerably across time and space, it is important to assess these potential impacts relative to the status of local deer populations. For instance, in regions of the southeastern United States where deer population declines have been documented during the past decade, timing of the observed declines appear to coincide with regional increases in coyote abundance. However, many factors may play a role in the recent decline across this region, including large-scale habitat changes associated with forest management during this time period, extensive establishment of pine plantations across the southeast during the 1980s has limited forage for deer, and extensive land development has reduced total acreage of available deer habitat. It is possible the synergistic effects of predation concurrent with these factors have contributed to recent regional declines in deer populations across the southeastern United States. Elsewhere where deer populations occur at low population densities (many of the Canadian provinces), predation has been shown to have additive effects on deer population growth and recruitment. Across the Midwest, deer population trends have remained stable or have increased since the early 1990s, despite documented increases in wolf densities and potential increases in coyote, bear, and bobcat densities. It is possible that increasing deer populations across the Midwest and Great Lakes regions have contributed to corresponding increases in predator populations. In Wisconsin, deer populations have continued to increase across much of the state since the mid-1990s, despite increasing wolf and bobcat (and arguably black bear) population densities. Though it's possible that coyote populations also have increased over this time period, distribution and abundance of coyote populations across Wisconsin has not previously been quantified. Consequently, the population status of coyotes across Wisconsin remains unknown. Importantly, predator populations (particularly wolves, bobcats, and black bears) across Wisconsin have likely been increasing slowly across the northern region of the state during the past 10–15 years, and parallel with increasing deer populations. However, it seems unlikely that predator densities increased appreciably in recent years, despite concerns that predators have contributed to reduced deer harvest during the past two years.

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Table 1. Summary of studies of predation in North American white-tailed deer populations. Estimates of percentages of adult and fawn mortality caused by predators are reported where available. Blank cells represent no data.

Lead author(s)	Study duration	Study Location	Deer population status	% Adult mortality caused by predators^a	% Adult killed by predators^b	% Fawn mortality caused by predators^c	% Fawns killed by predators^d	Primary predators causing mortality
Ballard et al.	1994-1997	New Brunswick, Canada	Declining			86.4	38.0	coyotes, bears, bobcats, domestic dogs
Brinkman et al.	2001-2002	Minnesota	Stable to increasing	12.5	1.3	66.7	10.3	coyotes, bobcat
Carroll and Brown	1971-1973	Texas	Stable			28.6-100	10-70	coyotes, bobcats
Cook et al.	1964-1965	Texas	Stable			82.8	59.3	coyotes
DelGiudice et al.	1991-1996	Minnesota	Stable	48.5	30.7			wolves
Hiller et al.	2004-2006	Michigan	Increasing			50	8.8	coyotes
Huegel et al.	1980-1983	Iowa	Stable to increasing			76.9	18.2	coyotes, domestic dogs

Table 1. Continued.

Lead authors	Study duration	Study Location	Deer population status	% Adult mortality caused by predators^a	% Adults killed by predators^b	% Fawn mortality caused by predators^c	% Fawns killed by predators^d	Primary predators causing mortality
Kunkel and Mech	1989-1990	Minnesota	Unstable			100	44.0	wolves, bears
Long et al.	1991-1995	Maine	Declining			47.1	27.6	coyotes
Nelson and Woolf	1980-1982	Illinois	Increasing			69.0	69.0	coyotes, domestic dogs
Ozoga and Verme	1980	Michigan	Enclosed and increasing			64.3	24.3	bears
Patterson et al.	1994-1999	Nova Scotia, Canada	Declining	37.0	23.9			coyotes
Pusateri Burroughs et al.	2001-2003	Michigan	Increasing			5.9	1.3	coyote ^e
Ricca et al.	1996-1998	Oregon	Endangered	3.3	1.6	56.8	33.3	bobcats, fox
Rohm et al.	2002-2004	Illinois	Stable to increasing			45.3	17.5	coyotes, bobcats, domestic dogs

Table 1. Continued.

Lead authors	Study duration	Study Location	Deer population status	% Adult mortality caused by predators^a	% Adults killed by predators^b	% Fawn mortality caused by predators^c	% Fawns killed by predators^d	Primary predators causing mortality
Saalfeld and Ditchkoff	2004-2005	Alabama	Increasing			41.7	27.8	coyotes
Sams et al.	1990-1992	Oklahoma	Increasing			75.9	28.9	coyotes, bobcat, gray fox
Vreeland et al.	2000-2001	Pennsylvania	Stable			6-37	3-17	Coyotes, black bears, bobcats
Whitlaw et al.	1994-1997	New Brunswick, Canada	Stable to slowly increasing	26-64	11-33			coyotes, bears, domestic dogs
Whittaker and Lindzey	1991-1992	Colorado	Increasing			79.2	51.4	coyotes

^aPercentage of documented adult mortalities attributed to predators; ^bPercentage of radiocollared adults killed by predators; ^cPercentage of documented fawn mortalities attributed to predators; ^dPercentage of radiocollared fawns killed by predators; ^eThough cause of death was reported as unknown, coyote predation was indicated as the suspected cause of death.

