Exhibit X

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Wolves–coyotes–foxes: a cascade among carnivores

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Abstract. Due to the widespread eradication of large canids and felids, top predators in many terrestrial ecosystems are now medium-sized carnivores such as coyotes. Coyotes have been shown to increase songbird and rodent abundance and diversity by suppressing populations of small carnivores such as domestic cats and foxes. The restoration of gray wolves to many parts of North America, however, could alter this interaction chain. Here we use a 30-year time series of wolf, coyote, and fox relative abundance from the state of Minnesota, USA, to show that wolves suppress coyote populations, which in turn releases foxes from top-down control by coyotes. In contrast to mesopredator release theory, which has often considered the consequence of top predator removal in a three-species interaction chain (e.g., coyote–fox–prey), the presence of the top predator releases the smaller predator in a four-species interaction chain. Thus, heavy predation by abundant small predators might be more similar to the historical ecosystem before top-predator extirpation. The restructuring of predator communities due to the loss or restoration of top predators is likely to alter the size spectrum of heavily consumed prey with important implications for biodiversity and human health.

Key words: coyote; fox; indirect effects; intraguild predation; mesopredator release; Minnesota, USA; predator interference; wolf.

Introduction

Cascading species interactions are critical to structuring ecological communities (Pace et al. 1999). Cascades are a type of indirect effect in which linear chains of direct effects propagate for three or more nodes (species or groups of species). Among trophic-level cascades are now well documented in both aquatic and terrestrial ecosystems (Terborgh and Estes 2010). Little attention, however, has been given to among-guild cascades. Such among-guild cascades whereby the largest or competitively dominant species directly suppresses a mid-sized guild member thus releasing the smallest guild member might importantly influence the composition of species guilds as well as the trophic levels above and below them.

As large predators are extirpated in certain parts of the world and recolonize in others, knowledge of such among-guild, or more specifically among-predator, cascades will be crucial to understanding and predicting changes in community composition. Among trophic-level cascades involving an apex predator that suppresses a smaller or mesopredator with consequent impacts on the mesopredator's prey have been well studied in recent years. Mesopredator releases have been documented in over 60 systems worldwide (Ritchie and Johnson 2009) in species complexes as varied as African lions (*Panthera leo*) and wild dogs (*Lycaon pictus*) (Creel and Creel 1996, Creel 2001) to black-backed gulls (*Larus marinus*) and crabs (Ellis et al. 2007). In North America, coyotes (*Canis latrans*) have been shown to suppress numerous smaller predators ranging from domestic cats (*Felis catus*) to opossum (*Didelphis virginiana*) (Crooks and Soule 1999, Ritchie and Johnson 2009), though their impacts on suppressing fox populations (*Vulpes vulpes*, *Urocyon cinereoargentus*, and *Vulpes velox*) are the most well documented (Harrison et al. 1989, Ralls and White 1995, Henke and Bryant 1999, Fedriani et al. 2000, Kamler et al. 2003, Mezquida et al. 2006, Karki et al. 2007, Moehrenschlager et al. 2007, Thompson and Gese 2007). The influence of coyotes in suppressing mesopredators has been shown to increase rodent and songbird diversity and boost duck nesting success (Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999). Separately, wolves (*Canis lupus*) in Yellowstone have been shown to suppress coyote populations (Berger and Gese 2007) leading to higher pronghorn (*Antilocapra americana*) calf survival (Berger and Conner 2008, Berger et al. 2008). An among-predator cascade by which wolves suppress coyotes thus releasing foxes has not yet been demonstrated but is plausible because niche overlap between wolves and coyotes, and between coyotes and foxes, is high relative to niche overlap between wolves and foxes. A high degree of niche overlap is expected to lead to higher rates of interference competition, including spatiotemporal avoidance, kleptoparasitism, and direct killing. We hypothesize that this will cause wolves to suppress coyotes, and coyotes to suppress foxes, more than wolves suppress foxes.

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In Minnesota, gray wolves were extirpated from nearly all of the state by the early 1970s (Mech 1970). Since the passage of the endangered species act in 1973, wolves have recolonized much of the northern-forested part of the state, and are now present, but at low abundance in the center of the state, which is transitional between farmland and forest. In the southern part of the state, which is largely farmland, wolves are not present. Here we make use of an over 30-year time series of wolf, coyote, and fox relative abundance to test the hypothesis that wolves suppress coyote populations, resulting in a cascading release of fox populations.

METHODS

The data

The Minnesota Department of Natural Resources began monitoring terrestrial carnivore populations in 1975 using scent station surveys (Sargeant et al. 1998). The scent station survey technique has been used to monitor foxes, coyotes, wolves, bobcats, and bears (Conner et al. 1983), which are difficult to survey using traditional methods (e.g., distance sampling, mark–recapture). Each scent station uses a fatty-acid tab to attract carnivores and sifted soil to record their tracks the following morning. Ten stations are placed on each 4.3 km long survey route for one night between late August and mid-October, which avoids pseudoreplication due to temporal correlation in visitation. All routes are separated by at least 5 km to avoid recording animals on multiple routes. The survey routes cover three geographically and ecologically distinct habitat zones of Minnesota (southern farmland, middle transition, and northern forest; Fig. 1A). In each habitat zone, we use the percentage of scent stations visited by foxes, coyotes, and wolves as an index of abundance for each species.

There are both red and gray foxes in Minnesota, but red foxes are historically much more abundant. Red fox harvests were 20–40 times higher than gray fox harvests until red fox entered a protracted decline in the mid-1990s from which they have not recovered (Fig. 1). The fox indices that we report are intended to be for red fox alone, but gray fox may represent a relatively stable background rate unlikely to influence our results. Gray fox tracks are differentiated from red fox by size and the presence of prominent nail prints and ridge on the interdigital foot pad.

Tests of this survey technique against independent estimates of population abundance have verified its use as a proxy of both seasonal and annual relative abundance (Conner et al. 1983). While scent station surveys reflect real changes in populations over time, their statistical power to detect changes in abundance is positively related to visitation rate (Sargeant et al. 2003). Thus, as visitation rate declines, more stations are needed to detect changes in abundance. When visitation rates are very low (1–5%), many hundreds of scent stations might be required to detect moderate changes in visitation rate (Sargeant et al. 2003). In order to meet statistical power requirements, therefore, the Minnesota Department of Natural Resources operates between 2500 and 4000 scent stations, divided among the three habitat zones.

The three habitat zones have qualitatively distinct canid communities allowing us to test hypotheses about the interactions among wolves, coyotes, and foxes. Wolves are absent in farmland, scarce in the transition zone, and relatively abundant in the northern forests. Foxes and coyotes are present in all three zones. Each species is cosmopolitan in their habitat requirements, with high densities occurring in both open and forested habitats in certain areas throughout their North American range. We analyze the canid time series in these three zones to test the among-predator cascade hypothesis: wolves suppress coyotes, which releases the fox population.

Statistical analysis

To test the among-predator cascade hypothesis, we analyze the 30-year time series of fox, coyote, and wolf relative abundance using two complementary statistical approaches. First, we examine how the abundance of each species changes with the abundance of other species in each habitat zone over the 30-year time series. Second, we examine how the year-to-year changes in population growth rate of foxes and coyotes are influenced by density dependence and the presence of the other species.

In the first approach, we examine the long-term population trends of each species (Fig. 1B–D) with respect to one another in each habitat zone using linear and quadratic regression analysis. In particular, we test whether there has been a significantly greater decline of foxes where coyotes are more abundant, and a significantly smaller coyote population increase where wolves are more abundant. We also explore interspecific correlations between the three species by regressing the relative abundance of each species against each other in each zone. Note that temporal autocorrelation can increase Type I errors, so we include a separate P value, P_{ac}, that accounts for temporal autocorrelation in the residuals by including a one-year lag term in the regression as indicated by the partial autocorrelation function.

In the second approach, we analyze fox, coyote, and wolf population time series with autoregressive linear models that test how the population growth rate of foxes and coyotes depends on intraspecific density dependence and interspecific competition. To demonstrate the biological relevance of our statistical models, we begin by modifying the discrete logistic growth equation for species n, where n can equal f or c for foxes and coyotes, respectively. The model is then given by

$$n_{t+1} = n_t \times \exp\left[a_n\left(1 - \frac{n_t}{K_n}\right)\right] = n_t \times \exp[\beta_{n0} + \beta_{n1} n_t] \tag{1}$$

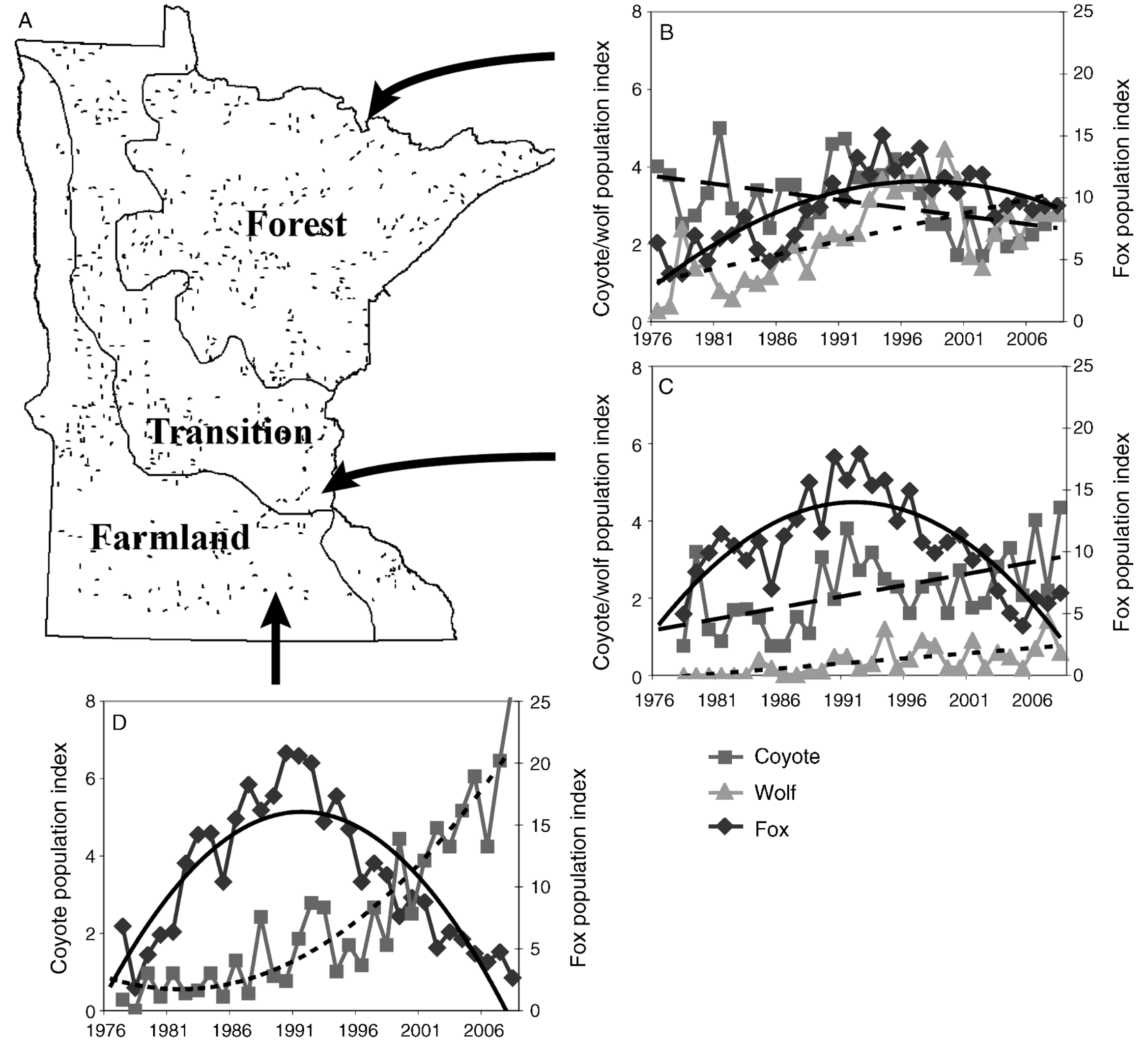

FIG. 1. (A) Map of carnivore scent station survey routes (black dashes) organized by habitat zones in Minnesota, USA, and (B–D) the corresponding time series of relative canid abundances, shown as unitless indexes. Best-fit lines shown are: solid, fox; dashed, coyote; dotted, wolf.

where n_t is the population index of foxes or coyotes at time t. The carrying capacity, K_n, and the maximum intrinsic population growth rate, a_n, are transformed into the regression coefficients β_{n0} and β_{n1}. Rearranging terms and taking the natural logarithm yields the log-difference equation

$$\ln \frac{n_{t+1}}{n_t} = \ln n_{t+1} - \ln n_t = \beta_{n0} + \beta_{n1} n_t. \tag{2}$$

Replacing the log-difference with $r_n(t) = \ln n_{t+1} - \ln n_t$ and using a Gaussian error structure, we derive the following regression model:

$$r_n(t) = \beta_{n0} + \beta_{n1} n_t + \varepsilon_{nt}$$

$$\varepsilon_{nt} \sim \mathcal{N}(0, \sigma_n^2). \tag{3}$$

The parameter β_{n1} can now be interpreted as the strength of density dependence of species n on itself.

To provide a biologically meaningful method for including as covariates the time series of species other than focal species n, we modify the discrete Lotka-Volterra competition equation for species n, with two competing populations, p_{1t} and p_{2t}. The model is given by

$$\begin{aligned} n_{t+1} &= n_t \times \exp\left[a_n\left(1 - \frac{n_t + \alpha_{n1} p_{1t} + \alpha_{n2} p_{2t}}{K_n}\right)\right] \\ &= n_t \times \exp[\beta_{n0} + \beta_{n1} n_t + \beta_{n2} p_{1t} + \beta_{n3} p_{2t}] \end{aligned} \tag{4}$$

where $\propto_{n1}$ and $\propto_{n2}$ are the competitive effects of species p_1 and p_2 on species n, and β_{ni} ($i = 0, \ldots, 3$) are regression coefficients. This equation leads to the more complete statistical model that can explore the strength of competition between foxes, coyotes, and wolves given by

$$r_n(t) = \beta_{n0} + \beta_{n1}n_t + \beta_{n2}p_{1t} + \beta_{n3}p_{2t} + \varepsilon_{nt}$$

$$\varepsilon_{nt} \sim \mathcal{N}(0, \sigma_n^2) \quad (5)$$

where β_{n2} and β_{n3} can be interpreted as the strength of the negative or positive impact of species p_1 and p_2, respectively, on the population growth rate of species n. We additionally include interaction terms in our final statistical model because nonlinearities in the population dynamics and/or the time series may exist.

We make inferences using corrected Akaike Information Criterion (AIC$_c$; Hurvich and Tsai 1989, Burnham and Anderson 2002). Specifically, we calculate the AIC$_c$ of models with all possible combinations of wolves, coyotes, foxes, and pairwise interaction terms in each zone. We use AIC weights to indicate our degree of confidence in each model relative to other potential models and we report the results for models with >15% AIC weight.

Using proportions as predictor variables can sometimes lead to violations of model assumptions such as normality of the residuals and constant variance. In these cases, proportions might need to be logit-transformed to map them to the whole real line. As such, we assessed residual and q-q plots using both proportions and logit-transformed proportions. Using proportions generally met model assumptions and using logit-transformed proportions did not change this. As such, we use raw visitation proportions as our index of population abundance throughout.

Hypotheses

Changes in the relative abundance of canids might be due to bottom-up changes in resources, interspecific interactions, or a combination of the two. Here, we consider three possible mechanisms: (1) a simple bottom-up model whereby populations of all three species in each zone increase when conditions are good and decrease when conditions are poor, (2) a habitat specific bottom-up model whereby bottom-up processes have primacy, but these vary according to habitat zone, and (3) an interactive model whereby changes in one or more canid populations directly or indirectly impact changes in another.

To provide support for the simple bottom-up model, we would expect populations of each species to be positively correlated throughout the state of Minnesota. To provide support for the habitat-specific model, we would expect populations of each species to be positively correlated within each habitat zone, but not necessarily across the entire state. To investigate whether certain species in one or more zones might be bottom-up regulated, we also used the winter North Atlantic Oscillation (NAO; Hurrell 1995) as a proxy for resource availability in our statistical analyses. While the NAO is not a direct measure of productivity, previous work has shown a strong correlation between the NAO and population dynamics of canid prey species in nearby areas such as snowshoe hare (*Lepus americanus*; Stenseth et al. 2004) and moose (*Alces alces*; Wilmers et al. 2006). As well, the NAO often predicts population dynamics data better than locally collected weather data (Stenseth et al. 2003). Finally, to provide support for the interactive model, we would expect some combination of negative and positive correlations among canid species. To support the among-predator cascade hypothesis in particular, we would expect wolves to have a negative and positive impact on coyote and fox populations, respectively, and for coyotes to have a negative impact on fox populations.

RESULTS

Changes in the relative abundance of wolves, coyotes, and foxes were best supported by the among-predator model over the bottom-up models. In the farmland zone, the fox population shows a strong decline as the coyote population grows (Fig. 2C). Conversely, in the forest zone where wolves are present, coyote and fox populations show no relationship (Fig. 2D), while wolves and foxes exhibit a strong positive relationship (Fig. 2E). The winter NAO was not a significant predictor in any of our regression models.

Population trends

The fox population trends in each zone were best explained by quadratic regression models with positive linear terms and negative quadratic terms (Fig. 1). The linear term in a quadratic model controls the slope of the initial population growth at population size zero. As the population size increases, the quadratic term begins to dominate the expression causing the population curve to bend over and decline. The more negative the coefficient on the quadratic term, the stronger the decline. Comparisons of the coefficients of the quadratic terms in the fox population trend in each zone indicate that the rate of decline is significantly higher in farmland over transition ($P < 0.01$), and in transition over forest ($P < 0.01$; Fig. 1). Corresponding to these fox trends, the coyote population increase was quadratic in the farm zone where wolves are absent ($P < 10^{-11}$, $r^2 = 0.86$), linear in the transition zone where wolves are slowly recovering ($P = 0.001$, $r^2 = 0.30$), and the coyote population decreased linearly in the forest zone where wolves have recovered strongly ($P = 0.02$, $r^2 = 0.17$), indicating top-down control of coyotes by wolves.

Population fluctuations

Examination of year-to-year changes in fox population growth rate revealed that the strength of fox density dependence in the single-species fox model (Eq. 1, $n = f$) was not significant and weakest in farmland, stronger in transition, and strongest in the forest, (Fig. 2A). The increase in the magnitude of the density-dependent coefficient, and variance of the model explained by density dependence (r^2) from farmland, where coyotes are abundant, to forest, where coyotes are relatively

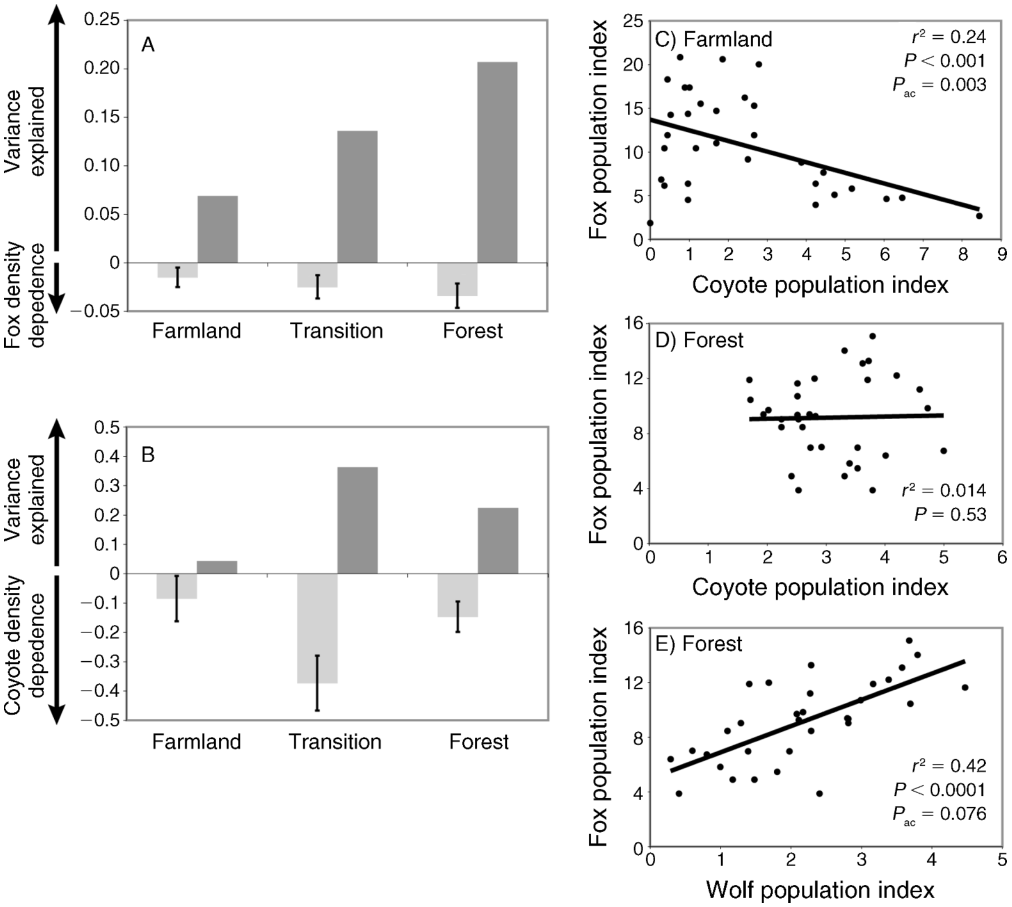

FIG. 2. Density-dependent effects of (A) fox and (B) coyote in the single-species models (Eq. 1), showing density dependence for fox (b_{f1}) and coyote (b_{c1}) and the proportion of variance explained (r^2) by the density dependence. (C–E) Linear regressions predicting fox populations across habitat zones in the presence of coyotes or wolves. P values corrected for autocorrelation in the residuals by including a lag term in the regressions are labeled P_{ac}. Error bars represent ±SE.

scarce, is suggestive of a release from interspecific competition with coyotes to self-regulation by foxes (Fig. 2A).

The strength of coyote density dependence in the single-species coyote model (Eq. 1, $n = c$) was weakest in forest, strongest in transition, and weak in farmland (Fig. 2B). This is generally consistent with the idea of bottom-up control in the farmland giving way to increasing among-predator control in the transition and the greatest among-predator control in the forest zone, with the exception that we would expect negative density dependence to be stronger in the farmland than in the transition. However, inspection of the coyote time series in the farmland reveals that the coyote population is still growing nearly exponentially so that this population has not yet experienced competition for food resources. Therefore it is not surprising that strong density dependence has not been achieved thus far in that zone.

The multispecies model predicting fox population growth rate (Eq. 2, $n = f$) revealed a strong negative effect of coyotes on fox population growth in the farmland zone, where wolves are absent (Table 1). This suggests that in the absence of wolves, coyotes strongly limit fox populations. In the forest zone with relatively abundant wolves, fox are released from top-down control by coyotes and show only a small positive correlation with coyotes (Table 1). This positive correlation is likely to come about when populations fluctuate in response to a shared food resource, a lower trophic level that we cannot explicitly account for in our model. In the transition zone, the best model explaining fox population growth rate included fox, coyote, and an interaction between the two (Table 1). This interaction reveals that when the coyote population is low, fox density-dependent effects dominate, but as the coyote population increases the fox population is regulated more by competition with coyotes than by density dependence.

Wolves did not have an important effect on fox population growth rate in the transition zone where they occur at low abundance. Wolves were not included in the best model ($\Delta AIC_c = 0$, AIC weight = 0.56) and while they revealed a small negative effect on foxes in the

TABLE 1. The best model or group of models explaining fox population growth in the farmland, transition, and forest zones of Minnesota, USA, by Akaike weight (w).

	Farmland ($w = 0.73$, $R^2 = 0.43$)		Farmland ($w = 0.25$, $R^2 = 0.45$)		Transition ($w = 0.56$, $R^2 = 0.43$)	
Covariate	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P
b_0	0.613 (0.146)	0.0003	0.683 (0.170)	0.0004	1.27 (0.299)	0.0002
f_t	−0.031 (± 0.009)	0.002	−0.040 (± 0.014)	0.01	−0.116 (± 0.028)	0.0003
c_t	−0.114 (± 0.028)	0.0003	−0.152 (± 0.054)	0.009	−0.429 (± 0.120)	0.001
w_t						
$f_t \times c_t$			0.006 (± 0.007)	0.42	0.039 (± 0.011)	0.002

Note: The covariate b_0 is the intercept parameter, f_t, c_t, and w_t, are the time-dependent fox, coyote, and wolf indices.

second best model ($\Delta\text{AIC}_c = 0.82$, AIC weight $= 0.37$), the effect was not significant ($P = 0.17$). Wolves, however, had a strong positive effect on fox population growth rate in the forest zone. In fact, the effect size is the strongest of any that we observe in any zone. The best model in the forest zone also includes a negative cross term for wolves and foxes, implying that as wolves increase, foxes are increasingly regulated by density dependence, which is evidence that wolves are allowing foxes to approach their carrying capacity. Direct inclusion of wolves into the multispecies coyote model (Eq. 2, $n = c$) did not reveal a significant negative effect of wolves on coyotes in either the transition or forest zones.

DISCUSSION

Taken as a whole, our analysis supports an among-predator cascade from wolves through coyotes to foxes. While the evidence we present is correlational, it is based on a plausible mechanism of increased interference competition between more closely sized canids. Wolves are more likely to kill coyotes than foxes because they might perceive coyotes as more direct competitors because of the coyote's larger size and more similar diet preferences. This mechanism is supported by data demonstrating wolf suppression of coyotes (Berger and Conner 2008, Berger et al. 2008) and separately, coyote suppression of foxes (Harrison et al. 1989, Ralls and White 1995, Henke and Bryant 1999, Fedriani et al. 2000, Kamler et al. 2003, Mezquida et al. 2006, Karki et al. 2007, Moehrenschlager et al. 2007, Thompson and Gese 2007). While bottom-up forces surely play a role in this system, neither the simple nor habitat specific bottom-up models were sufficient to explain the pattern of alternating negative and positive effects among these three canid species. Other alternative hypotheses explaining these data might include land use change as a driver of change in canid populations over time, and underlying habitat differences among the three zones. Neither of these alternative hypotheses stands up when confronted with all the available data. Land use change occurs too slowly to account for interannual variations in population growth, while habitat differences are unlikely to explain the patterns we report here as both foxes and coyotes have achieved high densities in both forested and farm habitats here and elsewhere (Kays et al. 2008). Finally, disease, particularly mange, likely impacts populations of canids in Minnesota, but without data we could not include this in our analysis. Qualitatively, it does not appear that shared disease drives the among-predator interactions because the canid populations do not exhibit a temporally correlated decline. The uniformity of the coyote increase and fox decrease is more consistent with direct killing of foxes by coyotes rather than interspecies pathogen transmission.

Size asymmetric among-guild effects whereby larger competitors suppress smaller ones have been shown in various taxa including plants (Schwinning and Weiner 1998), insects (Rosenheim 1998), and fish (Munoz and Ojeda 1998). Research in these systems has focused on pairwise interactions and their effects on lower trophic levels (e.g., Polis and Strong 1996, Sih et al. 1998). While the mechanisms driving among-guild interactions can vary from resource competition to interference competition or direct killing, our results indicate that indirect effects can cascade through a guild to impact the abundance of tertiary guild members. As a general rule, we would expect Fretwell's (1977) idea that the parity of a food chain determines the alternate suppression and release of plant biomass to apply to chains of among-guild interactions as well. Namely that among-guild interaction chains with even numbers of species will result in the smallest competitor being suppressed while among-guild interaction chains with odd numbers of species will result in the smallest competitor being released.

Our results indicate that the restoration of wolves to areas across the northern hemisphere might lengthen species interaction chains. This is likely to result in an increase in smaller predators (or those that like foxes are suppressed by coyotes but not wolves) in wolf occupied habitat, and consequent changes in prey community composition. As coyotes have expanded their range in the absence of wolves, the resulting exclusion of foxes is expected to lead to much lower predation rates on small mammals because fox densities are on the order of 5–10 fox families (2 adults and 4–6 kits per family) per 10 km^2 (Trewhella et al. 1988), but Eastern coyote densities are an order of magnitude lower at around 0.5 individuals per 10 km^2 in forested landscapes and around 1

Table 1. Extended.

Transition ($w = 0.37$, $R^2 = 0.47$)		Forest ($w = 0.51$, $R^2 = 0.52$)	
Estimate (SE)	P	Estimate (SE)	P
1.27 (0.293)	0.0002	−0.560 (0.345)	0.12
−0.115 (± 0.027)	0.0003	0.002 (± 0.032)	0.961
−0.398 (± 0.120)	0.003	0.093 (± 0.038)	0.021
−0.151 (± 0.106)	0.168	0.440 (± 0.143)	0.005
0.038 (± 0.011)	0.002	−0.031 (± 0.013)	0.031

individual per 10 km^2 in rural landscapes (Tremblay et al. 1998, Patterson and Messier 2001, Way et al. 2002). Small mammals are present in only 2–13% of Eastern coyote scats, but in 11–50% of red fox scats (Major and Sherburne 1987). The numerical and dietary difference between foxes and coyotes can combine to result in a markedly lower predation rate on small mammals when coyotes exclude foxes.

While the three canid species have some dietary overlap, wolves are most efficient at killing large prey such as ungulates; coyotes are most efficient at killing intermediate-sized prey such as lagomorphs, squirrels, and ungulate neonates; and foxes are most efficient at killing small prey such as small rodents, invertebrates, and birds, but also lagomorphs (Major and Sherburne 1987, Gompper 2002). As such the size spectrum of canid prey communities are likely to vary depending on whether wolves are present or not. In ecosystems with wolves, large and small prey will experience higher rates of predation than intermediate-sized prey, whereas in ecosystems lacking wolves, intermediate-sized prey are likely to experience higher predation rates (Fig. 3).

Consistent with this idea, there is evidence that the increasing coyote population (in the absence of wolves) has caused the decline of white-tailed jackrabbits over the past 40 years in the farmland and transition zones of Minnesota (Haroldson 2008). This decline may reflect a loss of preferred habitat, but a resurgence in jackrabbit populations during the peak of pelt prices in the late 1970s and early 1980s (when furbearers were heavily trapped) is suggestive of a temporary release from predation.

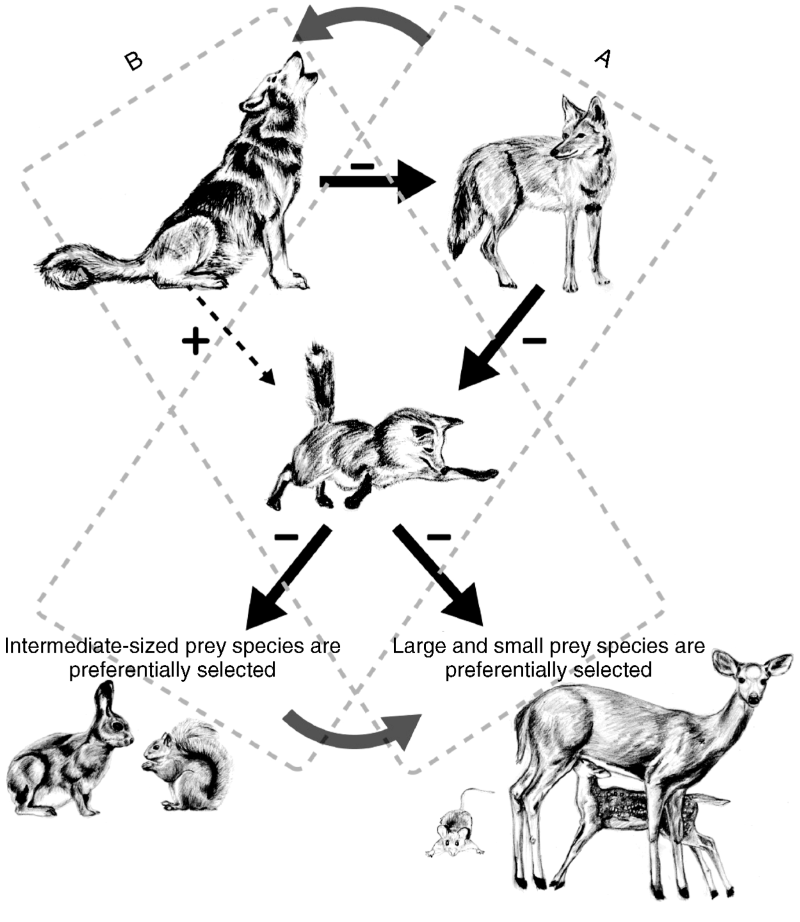

Fig. 3. Hypothesized impact of the among-predator cascade on food-web dynamics (with interactions indicated by black arrows). (A) Without wolves, coyotes suppress fox populations such that preferred coyote prey items are preferentially consumed by the canid guild. (B) With wolves, the interaction web transitions from A to B (indicated by the curved gray arrows). Coyotes are suppressed, releasing foxes and leading to dominant fox and wolf prey items being preferentially consumed.

The discovery of this among-predator cascade opens the door to search for similar types of cascades and to explore their implications. For example, the change in the size spectrum of preferred prey might importantly impact human–ecosystem interactions. Common prey species are often responsible for the emergence of zoonotic infectious diseases, including hantavirus and Lyme disease (Ostfeld and Holt 2004). For instance, the dominant reservoir hosts for Lyme disease in North America are small mammals (LoGiudice et al. 2003, Brisson et al. 2007), and deer are an important reproductive host for adult ticks. A wolf and fox dominated predator community is expected to preferentially prey on these important hosts, and prey less on the medium-sized hosts that are incompetent Lyme disease reservoirs (LoGiudice et al. 2003).

This among-predator cascade also informs our understanding of mesopredator release in terrestrial systems. Mesopredator release theory has often considered the consequence of top predator removal in a three species interaction chain (i.e., coyote–fox–prey) where the coyote was considered the top predator (Ritchie and Johnson 2009). However, the historical interaction chain before the extirpation of wolves had four links. In a four-link system, the top predator releases the smaller predator. The implication is that a world where prey species are heavily predated by abundant small predators (mesopredator release) may be similar to the historical ecosystem. As top predators recolonize their former ranges, ecological communities may be predictably restructured with consequences that are important to explore in future research.

Acknowledgments

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