

NUMERICAL AND BEHAVIORAL EFFECTS WITHIN A PULSE-DRIVEN SYSTEM: CONSEQUENCES FOR SHARED PREY

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Abstract. Some of the clearest examples of the ramifying effects of resource pulses exist in deciduous forests dominated by mast-producing trees, such as oaks, beech, and hornbeam. Seed production in these forests represents only the first of several pulsed events. Secondary pulses emerge as mast-consuming small rodents numerically respond to seed production and tertiary pulses emerge as generalist predators numerically respond to rodents. Raptors may also respond behaviorally (i.e., diet shifts) to subsequent crashes in small rodents following the crash phase in seed production. In oak-dominated forest in the Hudson Valley, New York, these various pulse and crash phases act synergistically, although not simultaneously, to influence thrush population dynamics through predation on nests, juveniles, and adults. As a consequence, factors limiting population growth rate and their age-specific action vary as a function of past acorn production. We highlight these interactions based on our eight-year study of thrush demography, acorn production, and small mammal abundance coupled with information on regional adult thrush population trends from the Breeding Bird Survey. We use these data sets to demonstrate the sequence of primary to tertiary pulses and how they influence breeding thrush populations. To extend our discussion beyond masting phenomena in the eastern United States, we briefly review the literature of alternative avian prey within pulsed systems to show (1) numerical and behavioral responses by generalist predators are ubiquitous in pulsed systems, and this contributes to (2) variability in reproduction and survivorship of avian prey linked to the underlying dynamics of the pulse. We conclude by exploring the broad consequences of cascading resource pulses for alternative prey based upon the indirect interaction of apparent competition among shared prey and the nature of temporal variability on populations.

Key words: *apparent competition; predation; resource pulse; temporal variability; trophic cascade.*

INTRODUCTION

Many terrestrial ecosystems are characterized by intermittent production of abundant resources for consumers, such as mast seeding and pulses of primary production following the unusually heavy rains (or droughts) of El Niño events (Ostfeld and Keesing 2000). Generalities are emerging in the ways in which consumer communities respond to these periods of feast and famine. A theory of resource pulses, i.e., periods of ephemeral resource superabundance followed by depletion through time, is now emerging that integrates concurrent theories of top-down and bottom-up control, direct and indirect effects on population dynamics, and temporal variation in interaction webs (Krivan and Schmitz 2003, Schmidt and Ostfeld 2003, Sears et al. 2004, Yang et al. 2008). Furthermore, a general pattern of resource pulses eliciting growth and subsequent decline in populations at several strongly linked trophic levels has now been observed in North America,

Eurasia, South America, and New Zealand (King 1983, Jaksic et al. 1997, Polis et al. 1998, Curran and Leighton 2000, Ostfeld and Keesing 2000, Stapp and Polis 2003, Yang 2004, 2006, Winder et al. 2005).

Some of the clearest examples of the ramifying effects of resource pulses exist in deciduous and coniferous forests dominated by mast-producing trees including oaks (McShea 2000, Schmidt and Ostfeld 2003), beech (*Nothofagus*; King 1983), hornbeam (Jędrzejewska and Jędrzejewski 1998), fir (Rimmer et al. 2001), and other boreal conifers (Koenig 2001, Koenig and Knops 2001). Although in most years these trees allocate accrued resources (carbon and nitrogen) largely to growth and maintenance, periodically, they shift their allocation to reproduction at the expense of growth (e.g., Sork et al. 1993). Seed production in these forests represents only the first of several pulsed events. Secondary pulses emerge as mast-consuming rodents (e.g., white-footed mouse, *Peromyscus leucopus*; eastern chipmunk, *Tamias striatus*; and red squirrel, *Tamiasciurus hudsonicus*) numerically respond to seed production and tertiary pulses emerge as generalist predators numerically respond to rodents (Elkinton et al. 1996, Ostfeld et al. 1996, 2006, Jones et al. 1998, McShea 2000, Schmidt et al. 2001a, b).

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Predators may also respond behaviorally to subsequent crashes in small rodents following low seed production or mast failure. The gross changes in food availability that accompany a crash of their primary (rodent) prey frequently cause predators to switch from selective to opportunistic diets during the transition of feast to famine (Dunn 1977, Jędrzejewska and Jędrzejewski 1998, Blomqvist et al. 2002, Schmidt and Ostfeld 2003). This can create a powerful one-two punch of resource pulses on shared, alternative (non-rodent) prey: (1) a numerical increase in predator abundance after a pulse in primary prey followed by (2) a crash in primary prey and expansion of the predator's diet to include alternative prey. Hence, the peak and crash phases of a resource pulse may act synergistically to influence alternative prey dynamics.

These direct and indirect effects following an initial pulse in mast production are the subject of our ongoing research on links between acorn production and songbird population dynamics. In our system, as in others, masting seed crops exert strong indirect effects on songbird populations mediated through small mammal and predator populations and their effects on nest predation, productivity (Ketterson et al. 1996, McShea 2000, Schmidt et al. 2001b), and juvenile survival in birds (Jędrzejewska and Jędrzejewski 1998, McShea 2000). A similar sequence of events is played out in primary prey–predator–alternative prey cycles, such as those involving lemmings–arctic fox–waders and waterfowl or voles–mustelids–tetraonids and songbird interaction webs. These cycles produce periods of ephemeral resource superabundance that differ from masting seed crops largely in the regularity of the former. The numerical and behavioral responses of predators described earlier characterize these systems as well (see Appendix A).

Two general conclusions are emerging from these studies: (1) despite variation in the details of individual studies, avian populations in forests dominated by mast-producing trees (or other sources of resource pulses) fluctuate between years of good and poor productivity; and (2) because of their role as shared alternative prey of generalist predators, and/or the episodic nature of the initial pulse, pulses in avian populations are greatly influenced by the inherent dynamics of the resource pulse. Hence, both the short- and long-term population growth rates of avian prey are affected by the characteristics (i.e., magnitude, timing, and variation) of the underlying resource pulse.

Here we examine primary, secondary, and tertiary pulses in acorns, mast-consuming rodents, and raptors, respectively, within in an oak-dominated deciduous forest. After examining the evidence for acorn mast-driven pulses in rodent consumer abundance, we focus on the effects of rodent consumers on songbirds. We hypothesized thrush (Turdidae) populations are influenced by rodents through the (1) direct effect of rodent predation, (2) density-mediated indirect effects of

rodents on other predators (i.e., predator numerical response), and (3) behavioral-mediated indirect effect of rodents on predator diet switching (see Fig. 1). To extend our discussion beyond masting phenomena in the eastern United States, we briefly review the literature of alternative avian prey within pulsed systems to show (1) numerical and behavioral responses by generalist predators are ubiquitous in pulsed systems and this contributes to (2) variability in reproduction and survivorship of avian prey linked to the underlying dynamics of the pulse. We conclude by exploring the broad consequences of cascading resource pulses for alternative prey based upon the indirect interaction of apparent competition among shared prey and the nature of temporal variability per se on populations.

METHODS

Study site

The Institute of Ecosystem Studies (IES), located in Dutchess County in southeastern New York, USA, contains approximately 325 ha of eastern deciduous forest dominated by oaks (*Quercus rubra* and *Q. prinus*) in the overstory (57–70% relative basal area; Jones et al. 1998). Oaks, sugar maple (*Acer saccharum*), and ironwood (*Ostrya virginiana*) are common understory trees, and maple-leaved viburnum (*Viburnum acerifolium*), witch-hazel (*Hamamelis virginiana*), and *Vaccinium* spp. are additional abundant woody species. Two 2.25-ha plots (150 × 150 m) were established in oak-dominated forest in 1991, and four additional plots were added in 1995. These six plots comprise three pairs (one control and one experimental plot) with >150 m separation between plots within a pair and >700 m separation between pairs. Since their establishment, the plots have been used as sites for monitoring acorn production and small mammal abundance, with the exception of acorn manipulation in two experimental plots in 1999 and mouse and chipmunk removal in three experimental plots in 1997 and 1998, respectively. For better estimates of small mammal abundance, we limit our analyses to the years 1995–2005 based on all six plots (except the years of manipulation when based on control plots only) and acorn production quantified on the two original plots from 1994 to 2004.

Acorn and small-mammal sampling

We quantified acorn abundance on each plot using 20 0.5-m² seed traps deployed under the canopies of randomly chosen mature seed-producing canopy trees, including *Q. rubra*, *Q. alba*, *Q. prinus*, and *Carya glabra* (pignut hickory). Traps were supported by monofilament lines attached to nylon stakes and were resistant to seed predators. We counted all intact, mature acorns and juvenile acorns separately for all traps during the autumn months of each year. Previous analyses demonstrated acorn production in *Q. rubra* has the biggest signal in affecting rodent abundance at IES (Jones et al. 1998), which may be linked to its abundance, perish-

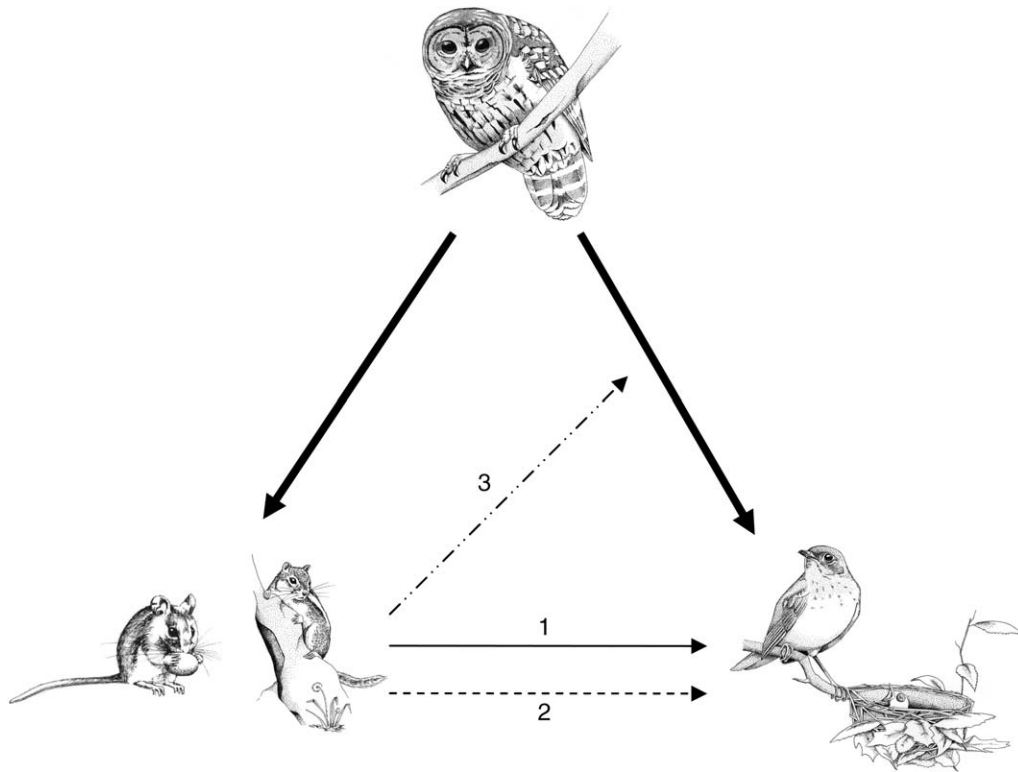


FIG. 1. Simplified schematic of the Institute of Ecosystem Studies (IES) system illustrating the three hypotheses tested: (1) direct effect, (2) density-mediated (i.e., numerical) indirect effect, and (3) behavioral-mediated indirect effect between rodents (white-footed mouse and eastern chipmunk) and thrushes (Veery is illustrated). The behavioral effect is mediated through diet changes in top predators, such as Barred Owls (*Strix varia*) as depicted here.

ability of acorns (*Q. alba* and *Q. prinus* germinate in the fall, *Q. rubra* in the following spring), and nutritional characteristics (Shimada and Saitoh 2006). Thus we estimated annual acorn production by averaging the number of intact, mature acorns from *Q. rubra* to derive mean acorn production per 0.5 m². These methods are appropriate for monitoring the temporal trends in seed production as we use it here.

We used the six 2.25-ha plots as sites for live-trapping rodents in order to estimate population sizes. Each plot consisted of an 11 × 11 array of trap stations with 15 m between stations (two traps per station, 242 traps per plot). Trapping was conducted for two to three consecutive days every three to four weeks, generally from May through November each year. We trapped small mammals (white-footed mice and eastern chipmunks) using two Sherman live traps (7.6 × 8.9 × 22.9 cm) baited with crimped oats (sunflower seeds and cotton added in colder months). Traps were set at 16:00 hours and checked between 08:00 and 12:00 hours the following morning. This schedule allowed us to capture both diurnal (chipmunks) and nocturnal (mice) species, which together accounted for >90% of captures. Small mammals were individually marked with metal ear tags and released at the site of capture. These protocols were

approved annually by an Institutional Animal Care and Use Committee.

Abundances of mice and chipmunks were estimated for each trapping period separately for each of the six trapping grids using the closed population robust design (Kendal and Nichols 1995, Kendall et al. 1995, 1997) as implemented in Program MARK (White and Burnham 1999). We use the same model for both mice and chipmunks. We set the probability of recapture equal to the probability of capture (i.e., no trap-shy or trap-happy animals), which was held constant in each year, but allowed to vary among years. The survival parameter was held constant during the trapping seasons, but overwintering survival rates were allowed to vary among years. Lastly, the probabilities of emigration and immigration were allowed to vary from each other and among years, allowing for potential emigration off of the trapping grids when, for example, densities were high.

Songbird monitoring

In 1998, we began monitoring the reproductive ecology of two forest thrushes: Veery (*Catharus fuscescens*), a small (28 g), predominantly ground-nesting thrush; and Wood Thrush (*Hylocichla mustelina*), a 48-g, predominantly shrub-nesting (nest height 2.51 ± 0.10

m [mean \pm SE]) thrush. From May through July each year, we searched the grounds (both on and off the plots) extensively for nests and monitored all active nests every three days (more often as they approached fledging) until depredated or until all fledglings had left the nest. Nests were considered successful if they fledged at least one young. Nests with obvious signs of predation or whose chicks disappeared before the earliest possible fledging date were considered depredated. We quantified annual rates of nest predation for each species as the nest daily mortality rate (DMR), calculated by dividing the number of depredated nests by the total number of nest exposure days (Mayfield 1975).

Regional population trends

We modified the methods used in Schmidt and Ostfeld (2003) to assess regional population trends in forest thrushes based on the Breeding Bird Survey (BBS). We used the original 20 BBS routes located within ~ 100 km of IES, a distance close enough for mast production to be synchronized (Koenig et al. 1999, Koenig and Knops 2000, Schaubert et al. 2002), and updated the data set to 2005 (previous analysis used BBS data from 1994 to 2000; Schmidt and Ostfeld 2003). However, whereas the earlier analyses used absolute population abundance, we now use annual population growth rate ($\lambda = [N_{t+1} - N_t] / N_t$) and change in abundance ($\Delta N = N_{t+1} - N_t$) of thrush species as our dependent variables. Based upon our previous studies, we hypothesized thrush populations are influenced by rodents through one or more of the following: (1) direct effect of rodent predation, (2) indirect (numerical) effect of rodents on other predators, particularly raptors, and (3) indirect (behavioral) effect of rodents on predator diet choice (Fig. 1). Because we did not obtain estimates of raptor abundance (or their diet) at IES we instead inferred the presence of these effects (hypotheses 2 and 3) through the relationship between λ (or ΔN) and rodent abundance. The direct effect (hypothesis 1) predicts a negative effect of rodent abundance in year t on λ . The numerical indirect effect (hypothesis 2) predicts a negative effect of rodent abundance in year $t - 1$ on λ , under the assumption that the numerical response of predators to rodents is reproductive with a one-year lag (see *Discussion* for further detail). The behavioral indirect effect (hypothesis 3) predicts a negative effect of a crash in rodent abundance between year $t - 1$ and year t on λ or, in combination with hypothesis 1, hypothesis 3 predicts a nonlinear (i.e., quadratic) relationship between λ and rodent abundance. In other words, rodent predation limits thrush productivity in high rodent years, whereas raptor predation limits thrush productivity in rodent crash years, and productivity is greatest at intermediate rodent abundance.

We calculated λ and ΔN for three species of forest thrush: Veery, Wood Thrush, and American Robin (*Turdus migratorius*). We used ANCOVA to regress λ

(or ΔN) against rodent density in year t (both linear and quadratic terms) and year $t - 1$. Species was included as a main effect, as were all interactions between species and main effects or covariates. All interaction terms were nonsignificant ($P > 0.15$; homogeneity of slopes) and hence were dropped from the final model. Rodent densities were calculated from averaging across the six 2.25-ha trapping grids for the approximate date of 12 June (i.e., mid-way through the songbird breeding season; Schmidt and Ostfeld 2003).

Literature review

Our literature review was intended to extend our discussion of resource pulses and avian populations beyond masting phenomena in the eastern United States. For the present discussion we limited our review to (1) documenting the presence of numerical and behavioral responses of generalist predators to pulses in primary prey (i.e., consumer) abundance and (2) quantify changes in predation rates on avian prey between years of extreme consumer abundance (i.e., peak vs. crash years). We focused on identifying studies demonstrating pulses in primary prey populations (e.g., rodents; second trophic level) rather than primary production (e.g., seed mast; first trophic level) since it is not always clear that pulses in prey populations are driven by their own resource availability, particularly within systems undergoing population cycles (Turchin 2003). Note, however, that pulses in primary prey are resource pulses to a generalist predator (third trophic level). We considered ephemeral predator-prey cycles, common to Holarctic populations of lemmings and voles, as pulses of primary prey, albeit the pulses occur with far greater regularity than episodic rodent outbreaks. However, we excluded snowshoe hare cycles that are characterized by a more gradual buildup and decline of hares (mean period of 8–13 years). This decision is based in part on Yang et al.'s (2008) characterization of resource pulses as being of short duration. How factors such as pulse duration and predictability (i.e., periodic vs. episodic) characterize the responses of organisms at higher and lower trophic levels is well worth exploring but beyond the aim of our brief review. Nonetheless, the behavioral and numerical responses we discuss below are common to snowshoe hare cycles and for that reason we direct the reader to several excellent examples (e.g., Keith and Rusch 1988, Doyle and Smith 2001, Krebs et al. 2001, Brook et al. 2005). Lastly, we restricted our review to avian prey since most predation on the pre-adult stages of birds (eggs, nestlings, fledglings, and juveniles) is by generalist predators. While non-avian alternative prey clearly exist (Norbury 2001, Kjellander and Nordström 2003, Prugh 2005), often in the same system, birds have often been easier to study because of the relative ease in observing and recording their reproductive success.

We began by searching the *Web of Science* for keywords including prey-switching, diet shift, resource

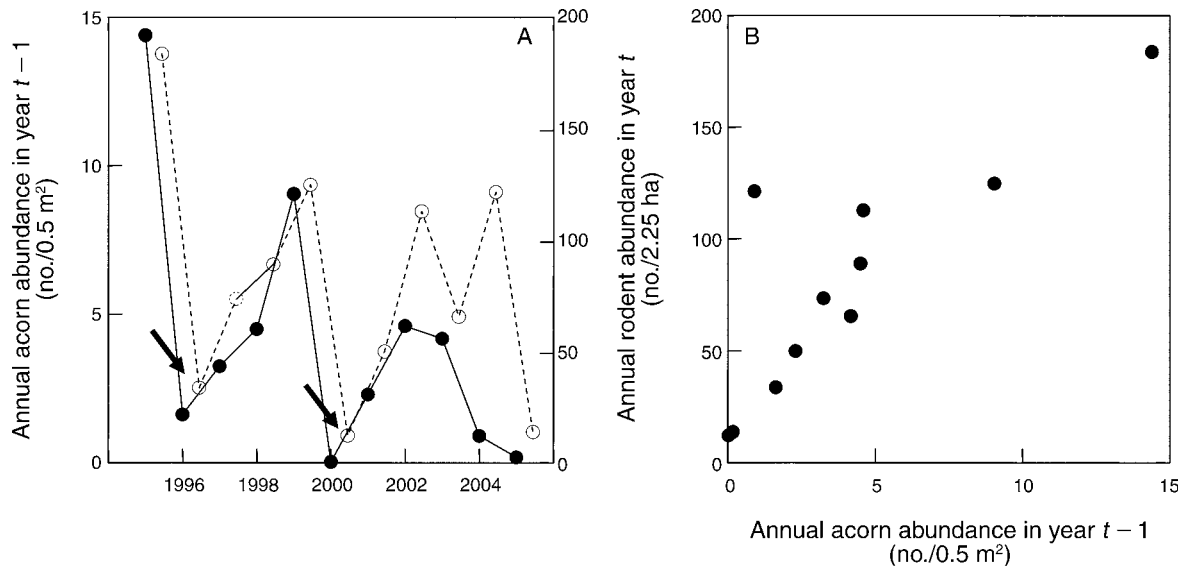


FIG. 2. Relationship between acorn and rodent abundance at IES shown as (A) variation through time and (B) correlation between the two variables. In panel (A), data are plotted with respect to the yearly spring (mid-June) estimate of rodent abundance (open circles). Acorn abundance (solid circles) was quantified in the previous fall and is slightly offset in time to reflect this. Arrows refer to two rodent population crashes for which regional thrush population data were available; shown within the dotted ellipses in Fig. 4.

pulse, and alternative prey hypothesis (APH). Similar to the hypotheses we developed above, the APH hypothesizes that synchronicity in alternative prey population dynamics is driven through functional and numerical responses of generalist predators to pulses (or more often cycles) in primary prey abundance (Angelstam et al. 1984, 1985). We followed up by reviewing works that either cited or were cited by papers referenced through the *Web of Science*. Every effort was taken to include data from statistically rigorous and independent data sets (i.e., many resource pulses or their underlying cause of population fluctuations may be spatial and temporally nonindependent [Koenig et al. 1999, Koenig and Knops 2000]). We also included studies of diet choice by predators on adult and juvenile birds, eggs, and nestlings, but these were limited to studies that contained one or more pulsed primary prey or studies self-described in some way as a test of the alternative prey hypothesis.

We used a subset of the studies (Appendix B) to quantify changes in predation rates on avian prey between years of extreme consumer densities (i.e., peak vs. crash years), including studies that reported predation rates on nests (including artificial nests in two instances), predation on adults, percentage of females without broods, or other metrics of predation. We did not use studies that solely reported patterns of abundance (e.g., proportion of first-year birds) because of the difficulty of distinguishing recruitment through reproduction vs. dispersal from other sites. Often predation rates were not explicitly reported but were displayed graphically. For these, we extracted predation rates from visual inspection of the figures. Appendix B

details these decisions for individual studies and discusses the possibility of biases.

RESULTS

Acorns to songbirds

We used linear regression to analyze the relationships between acorn (year $t-1$) and rodent abundance (year t) and between current rodent abundance and nest daily mortality rates on Veery and Wood Thrush. Rodent abundance was positively related to acorn abundance in the previous autumn ($P = 0.001$, $r^2 = 0.70$; Fig. 2). Nest predation, the principal cause of nest failure in the Veery, is highly variable from year to year and is an increasing function of current rodent density ($P = 0.005$, $r^2 = 0.70$; Fig. 3), whereas nest predation in Wood Thrush varied little among years and showed no relationship to rodent abundance ($P > 0.15$, $r^2 = 0.32$; Fig. 3).

Population trends

Thrush population growth rates were significantly affected by rodent abundance the previous year (significant quadratic term), but not by rodent abundance two years prior (Table 1). Both measures of thrush population growth were highest at intermediate rodent abundances and decreased when rodent abundance was low or high. Furthermore, the positive legs of the unimodal patterns in thrush population growth or change were driven by the two rodent population crashes occurring during our study period (see dotted ellipses in Fig. 4). After eliminating these two crash years in each analysis the quadratic terms dropped out as

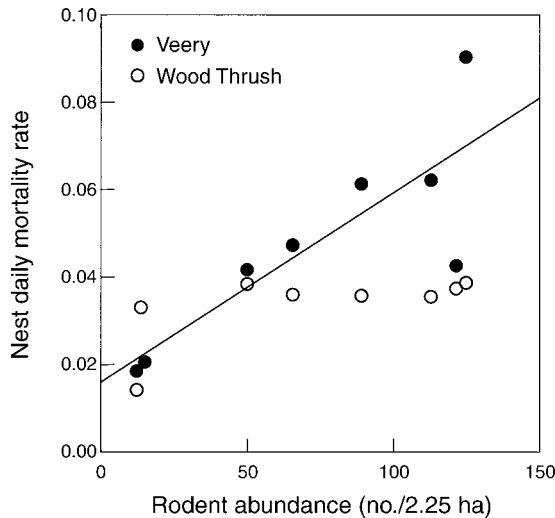


FIG. 3. Nest daily mortality rate (i.e., number of depredated nests divided by the total number of nest exposure days; after Mayfield 1975) of Veery and Wood Thrush as a function of current rodent abundance. A least-squares linear regression line ($P < 0.01$) is shown for the Veery. One data point (for Veery) was slightly offset to facilitate viewing.

nonsignificant ($P > 0.35$) and the regional population growth rate was negatively related to rodent abundance the previous year ($P = 0.001$) as expected in the absence of any indirect effect between rodents and thrushes. Lastly, all three species had similar population trends (Fig. 4) based on the absence of a significant species main effect (Table 1) or interaction terms including species ($P > 0.15$ and removed from the final model).

Literature review

Our review included 56 studies across 44 systems (Appendix A). Only 11 of the 44 systems examined the presence of both numerical and behavioral responses of predators: seven systems demonstrated both responses,

TABLE 1. Results of ANCOVA regressing regional thrush population growth rates, λ ($=N_{t+1}/N_t$), and absolute changes in abundance, ΔN ($=N_{t+1} - N_t$), against rodent abundance (one [t] and two [$t - 1$] years prior).

Effect	df	MS	F	P
λ ; $r^2 = 0.537$				
Species	2	0.002	0.18	0.841
Rodent (t)	1	0.035	3.26	0.085
Rodent ($t - 1$)	1	0.002	0.15	0.701
Rodent (t) \times rodent (t)	1	0.078	7.31	0.013
Error	21	0.011		
ΔN ; $r^2 = 0.438$				
Species	2	0.22	0.03	0.972
Rodent (t)	1	24.7	3.28	0.084
Rodent ($t - 1$)	1	1.95	0.26	0.616
Rodent (t) \times rodent (t)	1	47.4	6.29	0.020
Error	21	7.53		

Note: Regional thrush (American Robin, Veery, Wood Thrush) abundances were determined from Breeding Bird Survey routes. See *Regional population trends* for details.

one showed neither, and three showed a numerical but no behavioral response. However, the majority of studies either did not examine one or more effects or inferred effects statistically, as we have above. This often took the form of demonstrating a positive relationship between the current abundance of primary prey (e.g., lemming, voles, mice) and avian reproductive productivity. When such inferences are included, 35 of 40 (88%) and 22 of 25 (88%) systems reported evidence of behavioral and numerical effects, respectively.

The studies we reviewed showed a nearly universal short-term positive effect of pulses in primary prey on avian reproductive productivity, nest success (i.e., lower nest predation), and adult abundance with a one year time lag. However, the positive effect is, paradoxically,

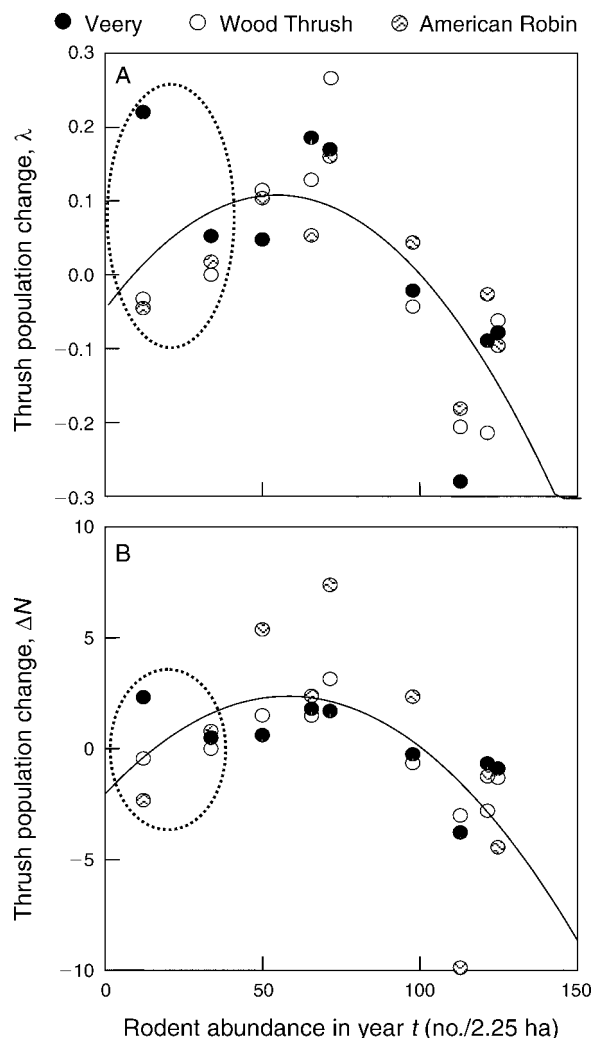


FIG. 4. Regional thrush (A) population growth rates, λ , and (B) absolute changes in abundance, ΔN , as a function of rodent abundance. A least-squares quadratic regression line is plotted through all the data points (species was not significant in each case; $P > 0.80$). Three data points were slightly offset to facilitate viewing. Data inside ellipses correspond to arrows in Fig. 2A.

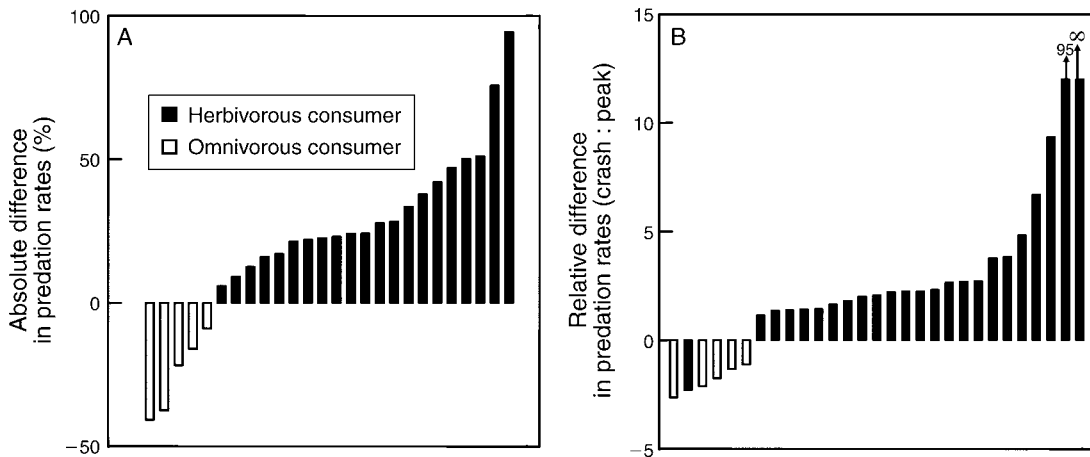


FIG. 5. Difference in predation rates on avian prey between crash and peak years of primary prey. (A) Absolute differences were calculated as the difference between crash year and peak year for studies that reported data as percentages; see Appendix B. (B) Relative differences were calculated as the larger of two ratios of predation rates: (1) crash years : peak years (displayed as positive values, i.e., predation was greater in crash years) or (2) peak years : crash years (displayed as negative values, i.e., predation was greater in peak years). Each bar represents an individual study or species ranked in order of lowest to highest difference within each panel. Herbivorous (e.g., lemmings and voles) and omnivorous (e.g., mice) consumer species are denoted by solid and open bars, respectively.

observed as an increase in avian predation precipitated by a crash in primary prey and diet-switching (selective to opportunistic foraging) in generalist predators. Excluding studies with omnivorous rodents that prey on birds themselves, predation rates on birds during rodent crash years increased by 2.86-fold, on average, above those experienced during rodent peak years (back-transformed mean of $\log[\text{relative difference}]$ excluding the highest and lowest studies for which the logarithm is undefined; see Fig 5A). Exceptions occurred when primary prey themselves consumed bird eggs, chicks, and fledglings (e.g., chipmunks) resulting in higher predation rates during peak rodent abundance, and rodent pulses in New Zealand *Nothofagus* forests (but see White and King 2006). It is very uncertain what the long-term effects of pulses in primary prey are on bird populations based on our review; a theme we revisit in the *Discussion* (see *Alternative prey in pulsed-driven systems*).

DISCUSSION

Our study supports two of our three hypothesized interactions between rodents and birds within a pulsed-resource system. First, we show strong direct and indirect evidence that rodents increased nest failure in Veeries (Fig. 3). The absence of a relationship between rodent abundance and nest predation in Wood Thrush is probably related to their larger body mass and greater nest height that allows Wood Thrush to defend and/or escape nest predation by primarily ground-foraging rodents. However, we believe rodents directly affect Wood Thrush reproductive productivity through fledgling mortality rather than nest failure. We recently completed a three-year radiotelemetry study on Wood Thrush fledglings across a temporal gradient of rodent

abundance at IES (2003–2005; see Fig. 2 for rodent abundance). During this study, we demonstrated high fledgling mortality and documented cases of chipmunk predation of fledglings predominantly during the rodent peak (Schmidt et al., *in press*). We have no data on the reproductive ecology of American Robins. Their larger body size (~80 g) and nests placed well above ground likely reduce the probability of nest predation, but we suspect they too are vulnerable to predation from rodents during the post-fledging period.

Second, we provide evidence that rodents indirectly affect songbirds through one or more response of generalist predators. First, we demonstrated a unimodal relationship between regional thrush population growth rates and rodent abundance. This is inconsistent with the pattern of reproductive productivity, which predicts a negative (or no) relationship between rodent abundance and thrush population growth. In particular, the positive leg of the unimodal pattern of population growth rate indicates that low or negative growth in thrush populations following crashes in rodent abundance requires other causes of mortality. Second, the synchronized population dynamics we observed are predicted by the alternative prey hypothesis (Angelstam et al. 1984, 1985, Lindstrom et al. 1987). APH posits that birds and other alternative prey are largely consumed during lean periods of primary prey when predators undergo diet-switching and that the birds are released in turn from heavy mortality as primary prey rebound. The resulting shifts in predation affect unique alternative prey simultaneously, thus synchronizing their population dynamics (Angelstam et al. 1984, 1985, Lindstrom et al. 1987, Small et al. 1993).

Both behavioral and numerical responses of raptors may have contributed to the unimodal pattern of thrush

population dynamics. However, we observed no effect of rodent abundance two years prior (i.e., through the delayed reproductive response of raptors) on adult thrush abundance as predicted if a numerical response by raptors to rodents occurred. This suggests that numerical responses were absent or relatively weak and that behavioral effects likely drive the pattern we observed. We did observe a numerical of response by Accipitrine hawks in an earlier analysis (Schmidt and Ostfeld 2003) using data from the Christmas Bird Count. However, winter abundance may not correlate well with more relevant spring abundance. Alternatively, accipiters may be less important than other shared avian or mammalian predators. For instance, our recent radio telemetry study on Wood Thrush fledglings identifies Barred Owls (*Strix varia*) and Broad-winged Hawks (*Buteo platypterus*) as important predators on Wood Thrush fledglings (Schmidt et al., *in press*).

Statistically, the unimodal pattern of population dynamics was identical among the three species of thrushes; however, visual inspection of the dynamics in Fig. 4 suggests that differences may exist. In particular, in the range of intermediate to low rodent abundance, Wood Thrush and American Robin show fairly steep declines in population growth rates with declining rodent abundance. In contrast, the Veery shows no such trend, although population growth rates are lower than would be expected in the absence of prey-switching (i.e., there should be a continuous increase in growth rate with declining rodent abundance). These small differences in dynamics between species are likely due to diet preferences in raptors. Veeries are relatively reclusive and smaller than Wood Thrushes and Robins. Given there exists a preference for larger passerines by the larger raptors (e.g., Jędrzejewski et al. 1994, Jędrzejewska and Jędrzejewski 1998) we suspect that this is responsible for some of the species differences in the avian growth rate curves.

Climate and food availability provide alternative hypotheses to explain regional synchrony seen among thrushes. Some variation in the magnitude of seed production in masting species is generally attributable to climatic variables (Koenig et al. 1996, Piovesan and Adams 2001, Schaubert et al. 2002), and may in fact underlie the patterns we observed. Mast and rodent abundance, however, remain proximal factors influencing thrushes. In contrast, the observation that thrush populations show similar unimodal patterns of abundance with acorn crops two years prior (Schmidt and Ostfeld 2003) is difficult to reconcile with variation in food availability driving the synchrony, but is consistent with the role of mast-consuming rodents. Last, the American Robin is a short-distance migrant, whereas Veery and Wood Thrush are Neotropical migrants that overwinter in southern Brazil (Remsen 2001) and Central America (Roth et al. 1993), respectively. All three species coexist for only the fraction of their annual cycle that corresponds with the breeding season. Yet

their populations show synchronous patterns of regional abundance in relation to breeding season factors (i.e., changes in rodent abundance in the wake of autumn acorn crops). These observations strongly suggest that their populations are influenced by events occurring in the breeding habitat (also see Summers et al. 1998, Holmes and Sherry 2001, Blomqvist et al. 2002), whereas nonbreeding-season events likely contribute to the variation seen among cycles (e.g., Schmidt and Ostfeld 2003).

Finally, similar effects of shared, generalist predators on avian prey have been noted widely in the literature. In Białowieża Forest in eastern Europe, for example, the assemblage of raptors consumes 45%, on average, of the spring–summer avian biomass (Jędrzejewska and Jędrzejewski 1998). Two species, Buzzard (*Buteo buteo*) and Tawny Owl (*Strix aluco*) are responsible for 71% of the predation. Tawny Owls consumed between 1.6 and 6.4 birds·ha⁻¹·yr⁻¹, with 98% of the variation in prey consumption explained by annual variation in the abundance of small rodents (Jędrzejewska and Jędrzejewski 1998). The relationship between avian predation and rodent abundance suggests a low threshold density of rodents below which predation on avian prey rapidly increases (Fig. 6). Thus owls (and martens) exerted their largest effects only after their mammalian prey crashed. Norbury (2001) showed a similar functional response of meso-predators (*Mustela furo* and *Felis catus*) on skinks (*Oligosoma* spp.) driven by rabbit (*Oryctolagus cuniculus*) abundance (Fig. 6). Rabbits, the primary prey of ferrets and cats, crashed in response to an infectious agent (rabbit haemorrhagic disease). Norbury's (2001) study did not include birds and thus was not included in the review; however his careful measurement of functional responses within a pulsed system complements those of Jędrzejewska and Jędrzejewski (1998). Indeed, the patterns shown in these two studies widely characterize those reviewed in Appendix A, but few researchers have explicitly measured functional responses as have Norbury (2001) and Jędrzejewska and Jędrzejewski (1998).

Alternative prey in pulsed-driven systems

In their reviews of resource pulses, Ostfeld and Keesing (2000) and Sears et al. (2004) point out the ubiquitous role of generalist predators in linking the dynamics of various species under temporal variability. In our system this includes mast-consuming rodents, which also prey on songbirds, as well as top predators, such as raptors, mustelids, and canids. Among years, one or more of these groups exert top-down effects on alternative prey, such that periods of feast and famine correspond to the presence and absence, respectively, of a (partial) temporal refuge from predation. But what is the effect of this variability on alternative prey, avian or otherwise? Are famine/predation years simply balanced by feast/refuge years, and populations insensitive to variability in the long term? We suggest two potential

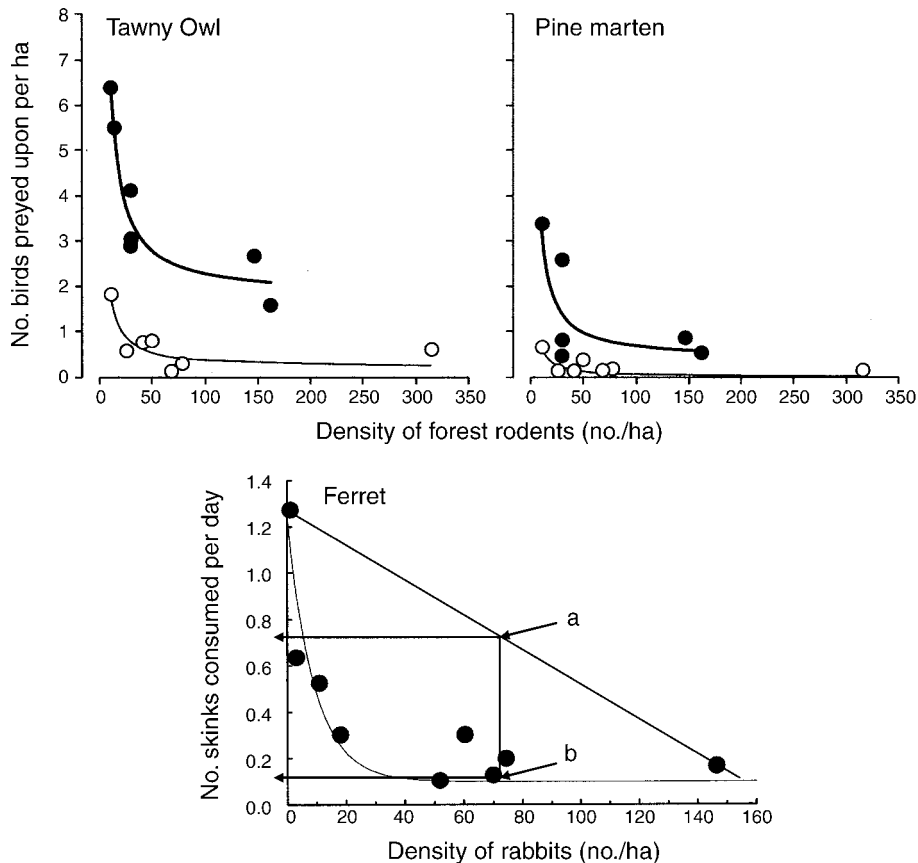


FIG. 6. Three examples of nonlinear predator functional responses to alternative prey as a function of the abundance of primary prey (solid and open circles in top panels represent spring–summer and autumn–winter data, respectively). The ferret example is used to illustrate Jensen’s inequality (i.e., nonlinear averaging) in a hypothetical case. Assume rabbit abundance varies uniformly between the minimum and maximum values observed, in which case the average value of rabbits (~75 individuals per spotlight kilometer) is given by b. However, because the relationship between skink consumption and rabbit abundance is nonlinear, the average mortality rate on skinks as a function of rabbit abundance is given by a and not b. The Tawny Owl and pine martin (*Martes martes*) examples are reprinted with kind permission of Springer Science and Business Media from Jędrzejewska and Jędrzejewski (1998: Fig. 5.37), and the ferret example has been modified and reprinted with kind permission of Blackwell Publishing from Norbury (2001: Fig. 2).

consequences of cascading resource pulses on alternative prey. The first is based upon the indirect interaction of apparent competition among shared prey. The second looks at the nature of variability itself on populations. In both cases, we explore what current ecological theory suggests might occur under variation in the frequency and magnitude of pulses.

The overriding importance of primary prey abundance on predation of alternative prey leads to a decoupling of the predator–alternative prey dynamic. In non-pulsed systems, rarity provides no relief to alternative prey from predation in the form of density-dependent mechanisms that reduce predation when alternative prey becomes uncommon and may result in apparent competitive exclusion (Anderson 1988, Courchamp et al. 2000, Jones 2003, Goodwin et al. 2005). However, within pulsed systems avian prey may find a partial refuge during periods with abundant consumers and selective foraging by predators. This

relief is temporary because predators will forage opportunistically following a consumer crash and this, together with a numerical response to the consumer pulse, will generate delayed apparent competition. Nonetheless, recent theoretical analyses (Abrams et al. 1998, Kimbrell and Holt 2005, Brassil 2006) of shared prey in temporally variable systems show two broad consequences for alternative prey: (1) some years, e.g., peak consumer abundance, provide birds with a temporary relief from predation by altering the topology of interaction webs when predators forage adaptively on a fluctuating prey base (Krivan and Schmitz 2003, Schmidt and Ostfeld 2003), and (2) the variability imposed through pulsed dynamics reduces the time-averaged abundance of predators (Abrams et al 1998) and creates asymmetries within nonlinear density-dependent processes (Jensen’s inequality; Ruel and Ayres [1999]). As a consequence, the intensity of apparent competition will be reduced or may even be

replaced by apparent mutualism. While temporal variability—the signature of resource pulses—is recognized as one form of dynamical instability, the variability itself may be vital for the persistence of alternative prey. These conclusions are tentative because theoretical analysis of the indirect effects among prey within pulsed systems is in its infancy and generally has operated under a restricted set of assumptions, including fixed density of alternative prey.

The discussion above suggests that variability can have a positive effect on prey persistence under shared predation. In contrast, studies of single species suggest a largely negative effect of variability. First, growth rates, λ , are a function of the geometric mean of conditions across all years, and the effects of bad years have a stronger impact on λ than do good years (Schmidt 2003). Storage effects (e.g., dormancy and caching) allow organisms to maintain populations through lean times and may be common in pulsed systems (Sears et al. 2004). However, birds, especially passerines, are relatively short lived and their ability to store reproductive success following good years is limited. Second, when density-dependent processes are nonlinear, population response to the average conditions is not equal to the response evaluated at the average of those conditions (Jensen's inequality; see Fig. 6). To use Norbury's example in Fig. 6, if rabbit abundance was fixed over time at the midpoint (we assume average, but it does not qualitatively change the implications) of observed rabbit abundances (point b), skink mortality from ferrets would be greatly reduced relative to the situation under temporal variability where rabbits fluctuate between ~0 and 150 (per spotlight kilometer); point a.

Nonlinearity can arise from a wide variety of processes. For simplicity, consider independent variability in predation risk and in food availability for passerines. If a high food year overlaps with high predation, birds may not be able to convert the fat times into reproductive productivity as a consequence of high nest and juvenile mortality. Likewise, birds may be limited in their ability to exploit the periods of high food abundance and low predation risk if there is a saturation of reproductive effort with food availability. Alternatively, intense density-dependence may follow a year of intense reproductive productivity that boosts population density and in turn creates further temporal variability. All of these scenarios are likely to create nonlinearity, invoking Jensen's inequality. Lastly, the effect of synchrony among putative competitor populations (Fig. 4) coupled with nonlinearity in interspecific competition can potentially add to negative effects manifested through resource pulses.

Norbury (2001) and Schmidt (2003) explored the effect of altering the regime of variability on skink and Veery populations, respectively, based on parameterized field data. Norbury's study was based on carefully measuring the functional and numerical responses of two generalist predators on rabbits (primary prey) and

skinks (alternative prey) rather than birds. He concluded that the optimal rabbit management policy for maintaining viable skink populations was to maintain low rabbit abundance and avoid large swings in rabbit abundance (i.e., control of infectious disease). Schmidt (2003) used data from studies on the reproductive ecology of the Veery in the northeast United States to link the long-term population growth rate of Veeries to the dynamics of acorn production. Results predicted that increases in the frequency of acorn masting would lead to significant declines in the long-term population growth rates of Veeries.

Clotfelter et al. (*in press*) observed such changes in the masting schedule of acorns in Virginia between the periods of 1980–1991 and 1992–2004, when the amplitude of periodic acorn masting events declined by >50%; the cause of this change remains uncertain. Similarly, in the first six years of their study on acorn masting, C. D. Canham and R. S. Ostfeld (*unpublished data*) observed three mast failures, whereas the following nine years produced only two failures. Only long-term data will indicate whether these temporal differences represent natural variation in the frequency of masting events or whether they are indicative of changes in the masting schedules. Nonetheless, given the demonstrated linkages between masting dynamics in trees and climate variables (Piovesan and Adams 2001, Schaubert et al. 2002), masting dynamics may be affected by future global climate change with strong consequences for avian populations.

In conclusion, a wealth of empirical studies and theoretical analyses suggest that the temporal variability inherent in cascading resource pulses can dramatically affect the abundance, stability and persistence of alternative prey populations. Still, few studies, including our own, have sufficiently detailed the numerical and behavioral responses of predators, their effects on alternative prey (Appendix A), or adequately tested the hypothesis of prey switching. We have enough information to understand the importance of resource pulses to populations and communities but are limited in our ability to predict organisms' responses should environmental change affect the magnitude and frequency of pulsed events. We hope our work stimulates others in this direction.

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APPENDIX A

Summary of the literature review examining numerical and behavioral responses of predators within pulsed systems and their impacts on the abundance and reproductive success of avian prey (*Ecological Archives* E089-036-A1).

APPENDIX B

Details for quantifying changes in predation rates between years of extreme consumer densities based on the studies in Appendix A (*Ecological Archives* E089-036-A2).