

# Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest

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## Summary

1. Synchronized mass production of seed crops, such as acorns, produces a resource pulse that may have far-reaching consequences for songbird populations through its effects on avian predators. Seed production in these forests represents only the first of several pulsed events. Secondary pulses emerge as mast-consuming rodents numerically respond to seed production and tertiary pulses emerge as generalist predators, such as raptors, numerically respond to rodents. In turn, these two groups reduce nest productivity and juvenile survivorship 1 and 2 years, respectively, after the initial pulse in seed production.

2. At our study site in south-eastern New York, USA, autumn acorn abundance (primary pulse) largely determines rodent abundance (secondary pulse) the following spring. We tested the hypotheses that the population dynamics of a shrub-nesting passerine (wood thrush *Hylocichla mustelina*), is influenced by rodents through the: (a) direct effect of predation by rodents; (b) indirect effect of rodents on the abundance of raptors (tertiary pulse); and (c) indirect effect of rodent abundance on raptor diet. The latter specifically hypothesizes that a crash in the rodent population in the wake of region-wide failure of acorn production leads to an extreme diet shift in raptors that increases post-fledging mortality in birds.

3. We conducted a 3-year study to examine variation in wood thrush nest success and fledgling survival, using radio telemetry, across a pulse of rodent abundance (i.e. low, medium and high). We also updated and reanalysed regional wood thrush population growth rates as a function of the annual variation in rodent abundance.

4. Fledgling survivorship, but not nest success, varied in relation to annual rodent abundance. Raptors and eastern chipmunks *Tamias striatus* were the most commonly identified predators on fledglings. Fledgling survivorship was greatest at intermediate rodent abundance consistent with a shift in raptor diet. Regional rate of wood thrush population growth showed a unimodal relationship with rodent abundance, peaking during years with intermediate rodent abundance. This unimodal pattern was due to wood thrush population growth rates near or below zero during rodent population crashes.

5. The telemetry study, pattern of regional abundance and synchronized population dynamics of coexisting thrushes suggest a common mechanism of behavioural changes in raptors in response to declines in rodent prey, which in turn affects thrush population dynamics.

**Key-words:** nest predation, post-fledging survival, resource pulse, temporal variability, wood thrush.

## Introduction

Cascades of direct and indirect species interactions are common in forests dominated by mast-producing trees, such as

oaks *Quercus* spp. (McShea 2000; Schmidt & Ostfeld 2003), beech *Nothofagus* spp. (King 1983) and hornbeam *Carpinetum* spp. (Jędrzejewska & Jędrzejewski 1998) that occur in many temperate deciduous forests throughout the world. Synchronized mass production of seed crops (mast events) produces an ephemeral superabundance of resources, or resource pulse

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(Ostfeld & Keesing 2000), that may have far-reaching consequences for songbird populations through the effects of the pulse on both mast-consuming rodents and their generalist predators (Jędrzejewska & Jędrzejewski 1998; McShea 2000; Rimmer *et al.* 2001; Schmidt & Ostfeld 2003, 2008). Secondary pulses emerge as mast-consuming rodents (e.g. white-footed mouse *Peromyscus leucopus* Rafinesque, eastern chipmunk *Tamias striatus* Linnaeus and red squirrel *Tamiasciurus hudsonicus* Trouessart, in North America) numerically respond to the production of seed crops, and tertiary pulses emerge as generalist predators (primarily raptors and mustelids) numerically respond to rodent outbreaks (Elkinton *et al.* 1996; Ostfeld, Jones & Wolff 1996; Ostfeld 1997; Jędrzejewska & Jędrzejewski 1998; Jones *et al.* 1998; McShea 2000; Rimmer *et al.* 2001; Schmidt & Ostfeld 2003; Clotfelter *et al.* 2007). Both rodents and generalist predators can significantly affect songbird populations through their effects on nest productivity, juvenile survival and adult survival (Dunn 1977; Jędrzejewska & Jędrzejewski 1998; Blomqvist *et al.* 2002; Schmidt & Ostfeld 2003; Schmidt 2003).

In oak-dominated forest in south-eastern New York, veery *Catharus fuscescens* (Stephens) and wood thrush *Hylocichla mustelina* (Gmelin) show divergent patterns of nesting success across temporal fluctuations of rodent abundance caused by variation in acorn mast (Schmidt, Ostfeld & Smyth 2006). Nest success in veery declines with rodent abundance, but the same is not true in wood thrush. When analysed as patterns of regional adult abundance (Schmidt & Ostfeld 2003, 2008), these two thrushes (and a third, the American robin *Turdus migratorius* Linnaeus) showed peak abundances in summers following intermediate (not low) rodent abundance (or 2 years after intermediate acorn abundance), whereas abundances are low following both low and high rodent (or acorn) abundance. The resulting unimodal pattern in abundance cannot be reconciled with annual variation in nest success or seasonal fecundity alone (Schmidt 2003). However, it may be related to changes in juvenile (i.e. post-fledging) survivorship in conjunction with changes in nest success that are jointly affected by rodent and raptor populations.

Raptor responses to pulses in rodent abundance may not be restricted to numerical (i.e. population growth) changes. During population crashes in small mammals that follow in the wake of region-wide failure of masting seed crops, raptors and other generalist predators often exhibit extreme dietary shifts from a rodent-dominated diet to a more generalized diet that includes a greater proportion of birds. In Białowieża Forest in eastern Europe, Jędrzejewska & Jędrzejewski (1998) documented an abrupt diet shift in the tawny owl *Strix aluco* (Linnaeus). Owl consumption of birds varied fourfold: between 1.6 and 6.4 birds ha<sup>-1</sup> year<sup>-1</sup>. Moreover, 98% of the variation in prey consumption was explained by annual variation in the abundance of small rodents. The relationship was strongly nonlinear: predation on avian prey steeply increased at relatively low rodent densities suggestive of a threshold effect (i.e. diet switching; Stephens & Krebs 1986). Thus, only after rodent populations crashed was owl predation on birds, largely juveniles, greatly inflated. Schmidt & Ostfeld

(2003, 2008) postulated that this same scenario occurs in oak forests in eastern North America. Higher fledgling mortality resulting from diet shifts by raptors may explain both the unimodal pattern in adult thrush abundance and the synchronized population dynamics among thrushes.

Based upon our previous studies, we hypothesized that wood thrush populations may be influenced by rodents through the: (1) direct effect of rodent predation (on nests and/or fledglings); (2) density-mediated indirect effect of rodents on the abundance of other predators (particularly raptors); and (3) behaviourally mediated indirect effect of rodent abundance on predator diet. To test these hypotheses, we conducted a 3-year study to examine variation in wood thrush nest success and post-fledging survival, using radio telemetry, across a pulse of rodent abundance: low (or crash), moderate and high (or peak) years. We also updated and reanalysed regional wood thrush population dynamics as a function of the variation in rodent abundance to better determine whether numerical (hypothesis 2) and/or behavioural (hypothesis 3) effects of raptors were present.

## Methods

### STUDY SITE

Our study was conducted in the c. 325 ha of eastern deciduous forest on the property of the Institute of Ecosystem Studies (IES; Dutchess County, NY). The forest at IES is dominated by oaks (*Quercus rubra* Linnaeus and *Q. prinus* L.) in the overstory. Oaks, sugar maple *Acer saccharum* (Marsh), and ironwood *Ostrya virginiana* (Mill) are common understory trees, and maple-leaved viburnum *Viburnum acerifolium* (Linnaeus), witch-hazel *Hamamelis virginiana* (Linnaeus) and *Vaccinium* are additional abundant woody species. We have studied the reproductive ecology of veery and wood thrush at IES since 1998. Presently, we restrict our study to wood thrush because this species is both abundant and large enough (c. 50 g) to equip with radio transmitters to measure fledgling survival.

### SMALL MAMMAL TRAPPING

Since 1995 we have maintained six 2.25-ha trapping grids to determine annual variability in small mammal (white-footed mice, eastern chipmunks, and shrews) abundance within the oak-dominated forest. Grids measured 150 m × 150 m and were arranged as an 11 × 11 array of trap stations (15 m between stations and two traps per station; 242 total traps per plot). Trapping was conducted for 2–3 consecutive days every 3–4 weeks generally from May through November each year using Sherman live traps (7.6 cm × 8.9 cm × 22.9 cm) baited with crimped oats. We set traps in the afternoon (c. 16.00 h) and checked them between 08.00 and 11.00 h the following morning allowing us to capture both diurnal (chipmunks) and nocturnal (mice) rodent species (> 90% of all captures). All rodents were individually marked with metal ear tags and released at the site of capture.

Mouse and chipmunk abundance were estimated separately for each trapping period and grid using the robust design model (Kendall & Nichols 1995; Kendall, Pollock & Brownie 1995; Kendall, Nichols & Hines 1997) as implemented in program MARK (White & Burnham 1999). We used the same model for both mice and chipmunks, setting the probability of recapture equal to the probability of capture (i.e. no trap-shy or trap-happy animals), which we held

constant in each year, but allowed to vary annually. We held the (apparent) survival parameter constant during the trapping season, but allowed overwintering survival rates to likewise vary annually. Emigration and immigration probabilities could vary from each other and among years, allowing for potential emigration off of the trapping grids during high-density years.

#### WOOD THRUSH NESTING SUCCESS

We monitored the reproductive ecology of the wood thrush annually from May through July by extensively searching suitable nesting habitat. Active nests ( $n = 36, 56$  and  $45$  for 2003–05, respectively) were monitored every 2–3 days until depredated or until all fledglings had left the nest. Nests were considered successful if they fledged at least one young. Nests with sign of predation or whose chicks disappeared before the earliest possible fledging date were considered depredated. We estimated the height of each nest based on the distance from the ground to the top of the nest rim.

#### TELEMETRY STUDY

When nestlings were approximately 12 days old (wood thrush brood young for 13–14 days on average, Roth, Johnson & Underwood 1996), one or two nestlings were removed, weighed to the nearest 0.5 g and banded with an aluminium US Fish and Wildlife Service band. Transmitters (Hoholil BD-2, including a temperature sensor, weighing 1.4 g; Hoholil Inc., Carp Ontario) were attached using the leg-loop method developed by Rappole & Tipton (1991). This attachment method uses a figure eight harness made with lightweight cotton embroidery thread to attach the transmitter to the back above the synsacrum. Transmitters weighed < 4% of juvenile body mass ( $35.4 \pm 0.24$  g) at time of attachment. Transmitter and harness systems weighing < 5% of nestling body mass do not adversely affect the survival of wood thrush during the post-fledging period (Anders *et al.* 1997). After outfitting young with a transmitter, each nestling was returned to the nest.

Fledglings were radio-tracked every 2 days over the course of the first 8 weeks post-fledging. We followed up abnormally low temperature readings (typically < 28 °C) by confirming the status of the bird and by identifying the source of mortality if a bird was dead. We followed up any loss of signal by repeatedly searching widely (at least 1 km from the nest or last known location) for the individual. Any permanent loss of signal during the first 3 weeks was considered a predation event; however, any fledgling that was not detected during the last two observation periods prior to this 3-week cut-off was censored at the last known observation period. We are confident in our conclusion of predation by this criterion since the overall detection probability was high; only 3.6% (24 of 661) of attempted sightings within the first 21 days failed to detect a bird that was later determined to be active. Furthermore, in practice all birds thus considered depredated had permanent loss of their signals by day 17, at least 5 days earlier than two independent studies that quantified the age of independence when juveniles disperse from their natal territory: 22.3 days (Anders *et al.* 1997) and 32.5 days (range 28–36 days, Vega Rivera *et al.* 1998). Because of the uncertainty of mortality (as opposed to dispersal) > 21 days post-fledging, we restricted our analyses of fledgling survivorship during the first 3 weeks.

To determine whether fledglings from the same brood could be considered as independent samples we assessed the proportion of the total variation in fledgling survivorship attributable to within (i.e. brood mates) vs. between broods. We applied a random-effects

general linear model in which survivorship (days) was treated as the dependent variable, individual nests were treated as fixed effects, and individual fledglings were treated as random effects (Proc VARCOMP, SAS 9.1). This model identified that differences in the survivorship within broods accounted for 83% of the total variation in fledgling survival. Based on the greater level of variation in survivorship within broods vs. between broods (approximately fivefold difference) we conclude that the independence of fates was upheld.

#### STATISTICAL ANALYSIS

We identified a priori four factors that might influence predation on wood thrush nests and fledgling survival. Factors included (some used in both analyses): (1) habitat (HABITAT); (2) nest height (HEIGHT); (3) nestling mass (MASS); (4) rodent abundance (linear and squared terms; RODENT and RODENT2, respectively). HABITAT (mesic vs. xeric) tests whether differences in predator assemblage or other habitat-related factors contribute to nest success or fledgling survivorship. Compared with xeric habitat, mesic drainages (containing standing or temporary pools of water) are characterized by fewer chipmunks (unpublished data) and greater activity of red-shouldered hawks and barred owls (KAS, pers. obs.). HEIGHT tests for an effect of nest height on nest success. Nests located higher above ground may experience lower predation from primarily ground foraging predators (Schmidt 2003), such as rodents and raccoons *Procyon lotor* (Linnaeus). MASS tests for an effect of nestling mass at the time of transmitter attachment on fledgling survivorship. RODENT (rodent abundance) tests for an effect of annual variation in rodent abundance on nest success or fledgling survivorship, whereas RODENT2 (rodent abundance, squared term) tests for a quadratic effect of annual variation in rodent abundance on fledgling survivorship (i.e. greatest survivorship at intermediate rodent abundance).

Given the high resighting probability of fledglings over the 21-day period (> 96%) we decided that application of formal mark and recapture analysis was not necessary for this study. However, due to logistical constraints, the interval between consecutive sightings varied between 1 and 5 days. In order to account for differences in the length of the period between consecutive nest checks and resighting intervals (for radio-tracked young) we estimated daily survival rates using the nest survival model of program MARK (White & Burnham 1999; Dinsmore, White & Knopf 2002; Rotella, Dinsmore & Schaffer 2004; Mong & Sandercock 2007). This procedure allowed us to model predation as a binomial process based on encounter histories developed for the nests and fledglings where events are scored either 0 (not depredated for nests, live for fledglings) or 1 (depredated for nests, dead for fledglings) and the number of trials is the number of days each nest/fledgling was observed/sighted. Encounter histories were coded with five pieces of information: (1) the date nest was discovered or the date of transmitter attachment; (2) the last day the nest or bird was known to be active; (3) the last day a nest was checked or a fledgling was searched for; (4) the fate of the nest or fledgling where 0 = survived and 1 = depredated or died; and (5) the number of nests or fledglings that shared the same encounter history. We calculated the number of days in each encounter history relative to the earliest date that a nest was discovered or a fledgling was radio-tagged. Within program MARK we constructed models using the design matrix tools and the logit-link function.

When modelling mark and recapture data a typical initial step involves testing the fit of the global model by calculating the variance inflation factor ( $c$ ) and then adjusting for any lack of fit. However, for the nest survival model these adjustments are not

possible because the global models are saturated and  $c$  cannot be identified (Dinsmore *et al.* 2002). As such, we used Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ; Akaike 1973, 1985) to compare models based on log-likelihood values (Burnham & Anderson 2002) and estimated model fit based on values of  $AIC_c$ , the number of parameters ( $K$ ), and the deviance (Dev). To create the most-parsimonious model, all possible combinations of independent variables were examined (Kleinbaum, Kupper & Muller 1988). Thus we generated a list of 15 candidate statistical models for the analysis of nest predation. This list is based on all combinations of the factors that may affect wood thrush nests and included a model with no factors (NULL model) and a model that contained all factors (the global model: GLOBAL). We followed a similar approach for the analysis of fledgling survival, in turn generating 12 candidate models. Models were ranked and compared using  $\Delta AIC_c$  and  $AIC_c$  weights, where  $\Delta AIC_c$  estimates the relative difference between the top ranked model and each other model, and  $AIC_c$  weights measure the weight in favour of the model given the data. Models with  $\Delta AIC_c \leq 2$  were considered to be equally parsimonious. However, if these models differed by only one predictor variable then we based model selection on model deviance with the better supported model having the lower deviance. When comparing a more complex model  $a$  to a simpler, less parameterized model  $b$  we employed information-theoretic evidence ratios ( $ER = AIC_c$  weight of model  $a/AIC_c$  weight of model  $b$ ) to quantify the relative support of model  $a$  vs. model  $b$ . We applied model averaging if several models were found to be equally parsimonious. Herein parameter estimates were weighted by the Akaike weight of the associated model and we calculated unconditional variance estimates to account for uncertainty in model selection. For each parameter we report 95% confidence intervals based on the unconditional variances. For each parameter estimated predictors were considered significant if the confidence intervals did not contain zero.

#### REGIONAL POPULATION TRENDS

We followed the methods used in Schmidt & Ostfeld (2003) to assess regional population trends in wood thrush based on data from the Breeding Bird Survey (BBS). This included using the original 20 BBS routes located within  $c.$  100 km of IES, a distance originally chosen arbitrarily, but close enough for most production to be synchronized (Koenig *et al.* 1999; Koenig & Knops 2000; Schaubert *et al.* 2002). We made the following changes to the analyses of Schmidt & Ostfeld (2003): (1) we updated the analyses to include data through 2005 (previous analysis used BBS data from 1994 to 2000), and (2) We used the annual population growth rate  $\lambda = [(N_{t+1} - N_t)/N_t]$  and absolute change in abundance ( $\Delta N = N_{t+1} - N_t$ ) of wood thrush as dependent variables, rather than relative population abundance ( $N_t$ ). Because we did not obtain estimates of regional or local raptor abundance we instead inferred the presence of these effects (hypotheses 2 and 3) through the relationship between  $\lambda$  (or  $\Delta N$ ) and rodent abundance. The direct effect (hypothesis 1) predicts a negative effect of rodent abundance in year ( $t$ ) on  $\lambda$ . (i.e. 1-year time lag). The numerical indirect effect (hypothesis 2) predicts a negative effect of rodent abundance in year ( $t - 1$ ) on  $\lambda$  (i.e. 2-year time lag), under the assumption that the numerical response of raptors to rodents is reproductive with a 1-year lag (see discussion for further details). The behavioural indirect effect (hypothesis 3) predicts a negative effect of a rodent crash between year ( $t - 1$ ) and year ( $t$ ) on  $\lambda$  or, in combination with hypothesis 1, a nonlinear (i.e. quadratic) relationship between  $\lambda$  (or  $\Delta N$ ) and rodent abundance in year  $t$ . A nonlinear relationship is expected if a rodent crash causes their

**Table 1.** Mean survivorship (CI; 95% confidence interval) of wood thrush (a) nests and (b) fledglings expressed as a function of annual rodent abundance (low, medium and high). Nest survivorship period of 21 days developed assuming mean clutch size of four eggs, 13-day incubation period and 14 days of brooding. All estimates derived from the model: RODENT

Rodent	Mean	95% CI	Mean	95% CI
(a) Nest survivorship				
Daily			(21-day period)	
Low	0.98	0.96–0.99	0.62	0.42–0.77
Medium	0.98	0.96–0.98	0.59	0.43–0.72
High	0.97	0.95–0.98	0.51	0.38–0.63
(b) Fledgling survivorship				
Daily			(21-day period)	
Low	0.98	0.94–0.99	0.69	0.47–0.83
Medium	0.99	0.94–1.00	0.79	0.54–0.92
High	0.96	0.92–0.98	0.47	0.30–0.63

predators to cross the threshold between selectively foraging on rodents and opportunistic foraging (i.e. Pulliam line; Pulliam 1974; Brown & Mitchell 1989). We regressed  $\lambda$  and  $\Delta N$  against rodent density in year  $t$  (both linear and quadratic terms) and year ( $t - 1$ ). Rodent densities were calculated from averaging across the six 2.25-ha trapping grids for the approximate date of 12 June, the approximate midpoint of the breeding season (Schmidt & Ostfeld 2003).

## Results

### NESTING SUCCESS

Wood thrush nesting success was relatively constant across the variation in annual small mammal abundance (Table 1a,b). Based on the best supported model (as identified by model deviance; Table 2a), nest success decreased with rodent abundance (coefficient:  $-0.12$ ; CI:  $-0.39$  to  $+0.16$ ). However, the coefficient reported above was not significant (i.e. included zero within the CI) and evidence ratios indicate the model that included rodent abundance was only moderately supported, 1.4 times more likely than either the null model or the models that included nest height or habitat alone.

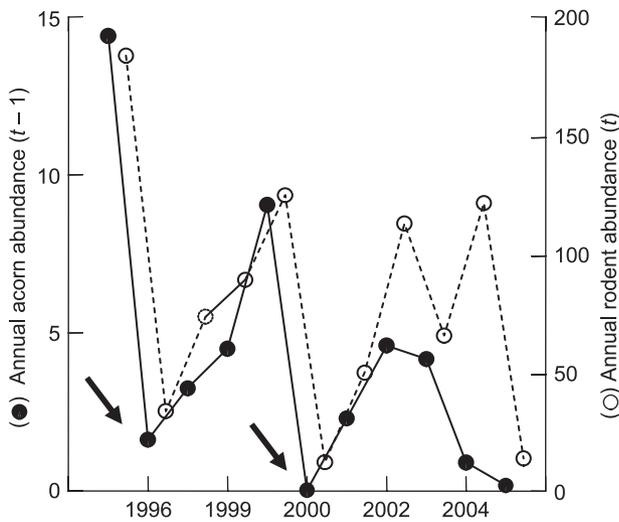
### POST-FLEDGING MORTALITY

Post-fledging survivorship was more variable among years than nest success (Table 1). Based on the model-averaged estimates derived from the best fitting models (those with a  $\Delta AIC_c \leq 2$  of the best supported model, collectively accounting for 76% of the total support; Table 2b) fledgling survivorship decreased relative to RODENT2 (coefficient:  $-0.41$ ; CI:  $-0.80$  to  $-0.02$ ) and fledgling mass (coefficient:  $-0.48$ ; CI:  $-0.81$  to  $-0.14$ ). Evidence ratios reveal that the best supported model was 2.64 times more likely than the model parameterized with MASS only, indicating a likely importance of rodents on fledgling survival. Fledgling survivorship was greatest at intermediate rodent abundance (Fig. 2). However, as year represents the appropriate sampling unit the short duration

**Table 2.** Model comparison for testing the effects of hypothesized independent variables on wood thrush (a) nesting success and (b) fledgling survivorship. All possible combinations of variables were compared; however, only models with  $w_i \geq 0.05$  are reported below

Model	LogL	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$	K	Dev
(a) Nesting success						
NULL	-215.59	433.17	0.00	0.34	1	431.17
RODENT	-215.22	434.46	1.28	0.18	2	430.45
HABITAT	-215.57	435.14	1.96	0.13	2	431.13
HEIGHT	-215.58	435.17	1.99	0.13	2	431.16
RODENT, HABITAT	-215.19	436.40	3.23	0.07	3	430.39
(b) Fledgling survivorship						
RODENT2, MASS	-107.51	221.04	0.00	0.29	3	215.02
RODENT, MASS	-107.87	221.75	0.71	0.20	3	215.73
RODENT2, MASS, HABITAT	-107.07	222.17	1.13	0.16	4	214.14
RODENT, MASS, HABITAT	-107.45	222.93	1.89	0.11	4	214.89
MASS	-109.52	223.05	2.01	0.11	2	219.04

Weight indicates weight of evidence of support for an individual model (sum of all weights = 1.00);  $K$  indicates the number of parameters for individual models; Dev indicates deviance.

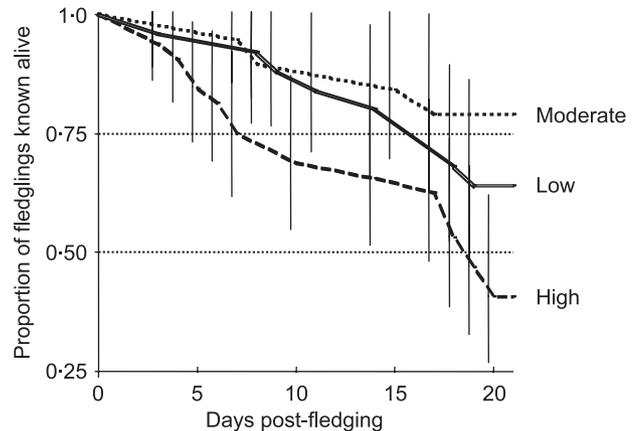


**Fig. 1.** Acorn and rodent abundance at IES from 1995 to 2005. Filled circles give the estimated autumn acorn abundance (for a description of the methods see Schmidt & Ostfeld 2003, 2008). Open circles give the estimated abundance of rodents for the following spring (mid-June), slightly offset from acorn abundance to reflect the later sampling dates. Arrows refer to two rodent population crashes for which regional wood thrush population data were available; shown in Fig. 3 as filled circles.

of the study precludes significance testing on the effects of rodent abundance.

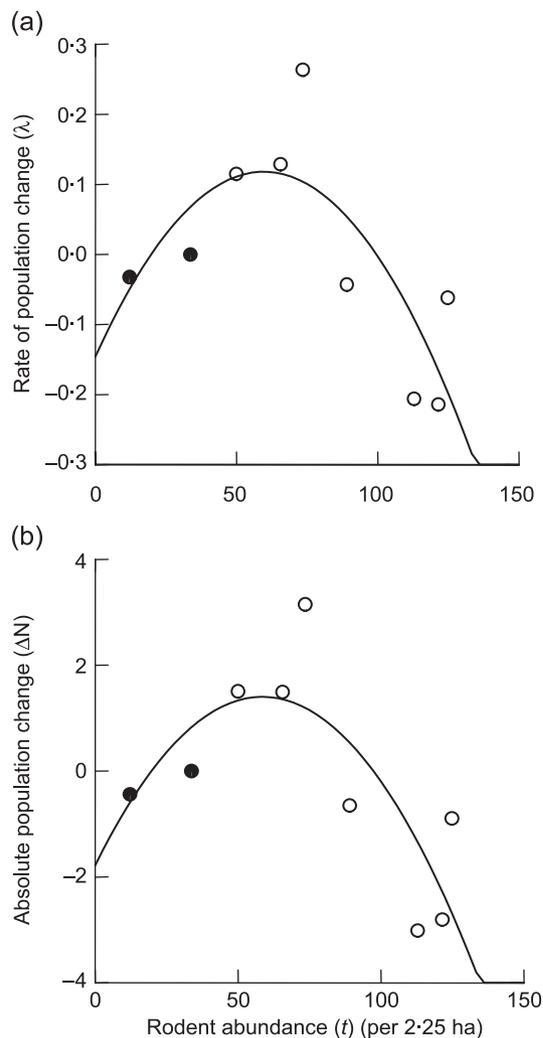
#### IDENTITY OF FLEDGLING PREDATORS

We observed a total of 26 mortality events out of 74 (35%) radio-tracked fledglings, but we were only able to identify the source of mortality in 11 of these. Chipmunk predation was identified by locating transmitters and bird remains in chipmunk burrows ( $n = 2$ ; high rodent year only). Hawk kills were identified (unknown species) by the presence of plucked feathers ( $n = 2$ ), and in three other instances were identified to broad-winged hawks *Buteo platypterus* (Viellot) based on the



**Fig. 2.** Proportional survival of wood thrush fledglings during the 21-day post-fledging period during years of low, moderate and high rodent abundance. Estimates of fledgling longevity were produced by back-calculating from the last day each fledgling was known alive. Longevity estimates were then pooled for each year of this study to produce a step function, where each loss of a fledgling reduced the proportion of total young known alive. Error bars indicate 95% confidence intervals.

presence of transmitters in or below a broad-winged hawk nest. Barred owl *Strix varia* (Barton) kills were identified based on the presence of transmitters in or below an owl nest ( $n = 2$ ) and in an owl pellet ( $n = 1$ ). One raccoon kill was strongly suspected by the presence of raccoon scat at the location of a chewed transmitter. The proportion of fledglings killed was greatest (55%) at high rodent abundance and, importantly, higher (32%) at low rather than medium rodent abundance (21%). Wood thrush fledglings can fly short distances within 1 week of fledging (Roth *et al.* 1996), after which their increased mobility allows for easier escape from ground-based predators. If we assume kills after day 7 were due to raptors, the percentage of raptor mortality was inversely proportional to rodent abundance (100, 75 and 64% in low, medium and high rodent year, respectively).



**Fig. 3.** Regional wood thrush (a) population growth rate,  $\lambda$ , and (b) absolute change in abundance,  $\Delta N$ , as a function of rodent abundance in year  $t$ . The solid line represents the significant least square quadratic regression. Filled circles represent the two crash years (see arrows in Fig. 1).

#### POPULATION TRENDS

Wood thrush population growth rate ( $\lambda$ ;  $r^2 = 0.623$ ) and absolute population change ( $\Delta N$ ;  $r^2 = 0.621$ ) were affected by rodent abundance the previous year with both significant (or near significant) linear (coefficient = 2.15,  $P = 0.053$ ; 2.26,  $P = 0.047$  for  $\lambda$  and  $\Delta N$ , respectively) and squared (coefficient = -2.72,  $P = 0.027$ ; -2.81,  $P = 0.024$  for  $\lambda$  and  $\Delta N$ , respectively) coefficients. In contrast, the regional wood thrush population was not affected by rodent abundance 2 years previously ( $P > 0.6$ ). The significant quadratic relationships were driven by declines in both in  $\lambda$  and  $\Delta N$  following the years with dramatic crashes in rodent abundance recorded during our study (Figs 1 and 3).

#### Discussion

Our study supports two of our three hypothesized interactions between rodents and wood thrushes within a

pulsed-resource system. Chipmunk predation on fledglings was directly documented during the high rodent year. In addition, rodent abundance (linear or squared term) was retained in the four best supported models (combining for 76% support) of fledgling survivorship. Second, regional wood thrush population growth rates were negatively correlated to rodent abundance above an approximate threshold of 20 rodents  $\text{ha}^{-1}$  (Fig. 3). In contrast, the current and previous analyses (e.g. Schmidt *et al.* 2006) have shown no significant relationships between rodent or chipmunk abundance and nest predation in wood thrush. Therefore, we conclude that rodents (chipmunks in particular) negatively affect wood thrush through consumption of fledglings but not nests. This pattern of mortality explains the negative leg of the unimodal pattern in wood thrush population growth and abundance (Fig. 3): post-fledging survivorship of wood thrush declines during periods of high rodent (chipmunk) abundance.

However, the positive leg of the unimodal relationship between regional wood thrush population growth and rodent abundance is inconsistent with: (1) the pattern of nest success alone, which predicts no relationship between rodent abundance and wood thrush population growth, and (2) the hypothesis that only chipmunk/rodent predation on fledglings covaries positively with rodent abundance, which predicts a strictly negative relationship between rodent abundance and wood thrush population growth. The low or negative growth rate of the regional wood thrush population following a crash in rodent abundance (filled circles in Fig. 3) requires an alternative source of mortality that increases as rodent abundance and rodent-based mortality decline. This source appears to be predominantly raptor predation on juvenile birds as raptors were the primary predator (of those identified) on wood thrush fledglings in our study and elsewhere (e.g. Anders *et al.* 1997).

Numerical responses of raptors may have contributed to the unimodal pattern if raptor abundance increased in the wake of peak rodent abundance and remained high as rodent abundance crashed. This indirect numerical effect (hypothesis 2) predicts rodent abundance 2 years previously will have a negative effect on  $\lambda$  (and  $\Delta N$ ). In our analysis of regional population trends we observed no such effect and conclude that a numerical response of raptors was absent or weak. Instead, our data are more consistent with an indirect effect of a crash in rodent abundance on wood thrush mediated by increased raptor attack rates (via diet choice; hypothesis 3). However, in the absence of direct data on raptor diet, our interpretation favouring the behavioural mechanism over the numerical mechanism is largely based on absence of evidence for the latter, and support from similar systems in which strong shifts in diet have been observed (e.g. Jędrzejewska & Jędrzejewski 1998; Norbury 2001; Schmidt & Ostfeld 2008).

Lastly, while the present study has focused exclusively on wood thrush, elsewhere we demonstrate that veery, American robin and wood thrush show synchronized population dynamics in relation to past rodent and acorn abundances (Schmidt & Ostfeld 2003, 2008). Synchronized population

dynamics are predicted by the alternative prey hypothesis (APH; Angelstam, Linström & Widén 1984), which posits that predation by generalist predators on birds (and other alternative prey) greatly increases during lean periods of primary prey (i.e. rodents) when predators switch their diet to alternative prey, including birds, and that predation on birds subsequently declines as primary prey rebound (Angelstam *et al.* 1984; Angelstam, Linström & Widén 1985; Lindström *et al.* 1987; Small, Marström & Wiilesrand 1993).

Fluctuating climate and food availability are viable alternative hypotheses that may explain the unimodal population dynamics and regional synchrony among thrushes. However, earlier analyses show that wood thrush populations have the same unimodal pattern of abundance with respect to acorn production 2 years prior (Schmidt & Ostfeld 2003). It is difficult to reconcile this time lag with variation in climate or food availability driving the synchrony, whereas the 2-year time lag is expected under the APH hypothesis with pulses of mast-consuming rodents. Taken together, the telemetry study, pattern of regional abundance, and synchronized population dynamics, all suggest a common mechanism of increased raptor predation during declines in rodent prey that is consistent with the majority of previous studies. For instance, Schmidt & Ostfeld (2008) reviewed 45 studies of avian populations breeding in communities that experienced dramatic annual pulses in rodent abundance. They reported a 2.86-fold, on average, increase in predation on birds during rodent crashes relative to peak years that was attributed to behavioural and numerical responses of generalist predators (largely raptors, mustelids and canids) in 88% of studies.

#### VARIATION IN POST-FLEDGING SURVIVAL IN SPACE AND TIME

The post-fledging period of passerines remains one of the least studied stages of avian ecology (Anders & Marshall 2005). This period has received little attention largely because the cryptic coloration and the mobility and secretive behaviour of young birds make it difficult to collect repeated observations of fledglings necessary to quantify their survival. As a result, estimates of spatial and temporal variation, patterns of reproductive productivity, and the processes that limit avian productivity are often based strictly on the number of young that are successfully fledged from the nest (reviewed in Anders & Marshall 2005). In the current study, we have shown that factors influencing the probability of nest success may not directly apply to the post-fledging period. Conversely, Rush & Stutchbury (in press) demonstrated forest fragment area effects on hooded warbler *Wilsonia citrina* (Boddaert) nest success but no such pattern in fledgling survival. We suggest that in general patterns of predation/survival during the post-fledging period may not mimic those of nest predation in both time and space. If true, then the extrapolation of nesting data for inferring population-level effects or evaluating ecological interactions will not be warranted.

In systems that experience resource pulses, it may be common for nest and post-fledging mortality to vary over

time (Blomqvist *et al.* 2002; Schmidt & Ostfeld 2008). As indicated above, this has practical considerations in estimating population vital rates. Less appreciated may be the variation in predation rates, the source of predation, and the primary stage that mortality is inflicted, each of which may have important evolutionary consequences. Fluctuating predation rates and sources of mortality select for differences in, for instance, patterns of nest dispersion (Hogstad 1995), the formation of protective nest associations (Larsen 2000), and patterns in clutch size (Julliard *et al.* 1997). In each of these examples, phenotypic variation was observed across gross temporal fluctuations in the abundance of small mammalian prey for mustelids (Hogstad 1995; Julliard *et al.* 1997) and jaegers (Larsen 2000), which led to variation in predation rates and the source of predation. With the advent of smaller radio technology and an increase in studies on post-fledging ecology we are likely to observe frequent phenotypic adjustments in avian reproductive strategies due to the changing nature of predation across developmental stages and through time in pulsed systems. A greater focus on temporal variation across the entire avian life cycle will enhance our understanding of avian population dynamics, phenotypic plasticity, and life-history strategies.

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