A food pulse drives conflicting fecundity and nest-site constraints for a cavity-nesting bird

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Nestweb

Secondary Cavity Nesters

- Bushy-tailed Woodrat
- Red Squirrel
- Northern flying Squirrel
- Mountain Chickadee
- Tree Swallow
- Mountain Bluebird
- European Starling
- Northern saw-whet Owl
- American Kestrel
- Bufflehead
- Barrow's Goldeneye

Primary Excavators

- Black-backed Woodpecker
- Three-toed Woodpecker
- Hairy Woodpecker
- Red-naped Sapsucker
- Northern Flicker
- Pileated Woodpecker
- Natural

Facultative Excavators

- Black-capped Chickadee
- Downy Woodpecker
- Red-breasted Nuthatch

Nest Use (proportion) (N = 2503 nests)

- < 0.10
- 0.10 - 0.49
- 0.50 - 1.00

revised from Martin et al. 2004
1995-2010

Trees

- Pine (68)
- Aspen (2399)
- Spruce (13)
- Cottonwood (2)
- Fir (21)
Mountain pine beetle (*Dendroctonus ponderosae*): a food pulse in the nestweb

- Year-round food supply for cavity producers, competitors and predators
- Red-breasted nuthatch (*Sitta canadensis*)
  - irruptive, resident, bark insectivore, facultative excavator
Cavity-nester densities ↑ with beetle

Norris & Martin Oikos 2010
Nuthatches followed the food

Decayed aspen trees

Beetle-infected pine

Norris & Martin. 2008 J. Wildl. Mgmt.
Questions

- Excavate more cavities?
- Fecundity increase?
- Nest survival decline due to inc comp & pred?
Methods

• 418 nuthatch nests
• 30 sites, 1995-2009
• fecundity (# eggs, hatched, fledged...)
• Population densities: point count surveys
• Veg surveys: cavity, tree & habitat characteristics
Mixed model approach:
1. Excavation?
2. Fecundity?
3. Nest survival?

\[ y \sim \beta_o + \beta_a a + \beta_b b + \beta_c c + \beta_d d + (1 \mid Z) \]

- Excavation:
  - # eggs laid
  - Julian hatch date
  - # hatched
  - # fledged
- Beetle abundance
- Cavity “freshness”
- Clutch size
- Julian hatch date
- Nuthatch pop density
- Squirrel pop density
- No. visits
- 2° interactions

(Poisson, Quasipoisson, Normal, Binomial distributions)
Six best fit models for each response variable

\[ y \sim \beta_o + \beta_a a + \beta_b b + \beta_c c + \beta_d d + (1 \mid Z) \]

E.g., No Fledged \sim Beetle + Nuthatch density + Squirrel density \mid Site/TreeID

<table>
<thead>
<tr>
<th>Fixed effect</th>
<th>Parameter estimate</th>
<th>Standard error</th>
<th>DF</th>
<th>t-value</th>
<th>p-value</th>
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<tbody>
<tr>
<td>(Intercept)</td>
<td>1.56</td>
<td>0.05</td>
<td>115</td>
<td>33.99</td>
<td>0.000</td>
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<tr>
<td>Beetle_{t-1}</td>
<td>0.05</td>
<td>0.02</td>
<td>29</td>
<td>2.45</td>
<td>0.021</td>
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<tr>
<td>Nuthatch density</td>
<td>0.36</td>
<td>0.17</td>
<td>29</td>
<td>2.11</td>
<td>0.044</td>
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<tr>
<td>Squirrel density</td>
<td>-0.26</td>
<td>0.14</td>
<td>29</td>
<td>-1.94</td>
<td>0.063</td>
</tr>
</tbody>
</table>
More new excavations at sites and in years with high beetle abundance

\[ \beta_{\text{intx}} = 4.58 \pm 2.19, \ p = 0.04 \]
Earlier nests & no cost of later nests

\[ \beta_{\text{Intx}} = 1.88 \pm 0.78, \ p=0.02 \]
Nest survival declined as pops & beetle inc.

\[ \beta_{\text{Intx}} = -12.7 \pm 4.7, \ p=0.009 \]
Summary

- Beetle outbreak increased fecundity for nuthatches
- As pops inc., high comp for cavs & pred in beetle patches → excavation
- Smaller clutches associated w later breeding in new cavs ameliorated with beetle
- Higher pred where beetle high, as densities increased: density dependent nest predation
- Nuthatches traded off low nest predation risk & low cavity availability for food availability
Conservation Implications

• Insect outbreaks influence complex interactions between resource constraints & species interactions
• Other species, such as non-excavators may not be as resilient (e.g., Aitken & Martin 2008)
• Retention of current and future cavity-bearing trees may be essential for long-term maintenance of cavity-nesting communities
TAKE-HOME MESSAGE:

- More new excavations
- Higher reproductive output
- Increased predation
Acknowledgements

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Future research

• Climate change may increase the intensity, frequency & synchrony of resource pulses → cascading effects on communities (Yang & Rudolf 2010 Ecol Lett)
• Irruptive populations resilient to change, but this is dependent on heterogeneous disturbance across landscapes
• What are the long-term, broad-scale implications of synchronous resource pulses on communities?
Resource pulses

- Direct, bottom-up effects
- Indirect, top-down effects

Fig. 1. Conceptual model of the effects of pulsed resources permeating through a food web. The direction of arrows represents the direction of causal change in abundance or biomass. Solid lines indicate a positive effect and broken lines indicate a negative effect of one trophic group on another.

Ostfeld & Keesing (2000)
Determining factors

Food pulse

Cavity availability
- Population density
- Nest predation risk

Population density

Nest predation risk

Earlier nest
- Clutch size
- Nest predation

Later nest
- Clutch size
- Nest predation

Decision to excavate

Use old cavity

Excavate new cavity

Reproductive consequences
Nest survival low in forest interior

\[ \beta = -0.01 \pm 0.004, \ p = 0.007 \]