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Bruce E. Kendall, Stephen P. Ellner, Edward McCauley, Simon N. Wood, Cheryl J. Briggs, William M. Murdoch, and Peter Turchin. 2005. Population cycles in the pine looper moth: dynamical tests of mechanistic hypotheses. ***Ecological Monographs*** **75:259-276.**

Appendix E. Incorporating the effects of insecticide spraying

In some instances forests were sprayed with insecticide in response to severe *Bupalus* outbreaks. Our models treat effects of spraying as part of the "process noise," which is not entirely valid given that spraying only occurs when pupal density is exceptionally high. In particular, the largest observed density at Tentsmuir (62.7 pupae/m^2 in 1984) provoked aerial spraying of the entire forest (Straw 1996) and was followed by a rapid collapse to 1.3 pupae/m^2 in 1985. Localized spraying in forest "compartments" with high pupal density occurred during two other large outbreaks in Tentsmuir (16.1 pupae/m^2 in 1957, 12.3 pupae/m^2 in 1997), and both Cannock and Culbin were sprayed with DDT in response to the buildup in 1953 (Crooke 1959).

This argues for extending the models to explicitly include spraying in response to large outbreaks. However, spraying is a relatively rare event. Based on the available literature (Crooke 1959, Scott and Brown 1973, Straw 1996) it appears that there were only 4 occasions ($< 4\%$ of the data) when significant spraying operations were undertaken in response to high pupal density. It is therefore likely that the additional parameters required to model spraying and its consequences would have very minor effects on the models' overall goodness-of-fit.

To explore this issue we used a simple model of spraying. Based on the information provided by (Straw 1996) for Tentsmuir and the mean pupal densities observed during spraying years, we assumed that spraying is likely (probability of spraying=2/3) if mean pupal density gets above 12/m^2, and is certain if mean pupal density is above 12/m^2 for two consecutive years. We then add one more parameter to each model, the 'spray effectiveness' ϵ. Although the fraction of the forest sprayed was variable (because spraying was targeted at areas of high density) it is a reasonable first approximation to assume that spraying imposes a constant additional mortality on the affected stage, larvae in the following generation. Spraying was timed to kill first and second instar larvae, so we assume that spraying mortality acts before density-dependent larval mortality.

- In the parasitoid model, the additional mortality is imposed in between Eqs. (4) and (5) [throughout this Appendix, equation numbers refer to equations in the body of the paper]. So in years when spraying occurs, Eq. (4) is replaced by
$$L_{t+1} = (1-\epsilon)A_t e^r. \qquad (1)$$
- Similarly, in the Food Quality model, Eq. (20) is replaced by
$$L_{t+1} = (1-\epsilon)R(A_{(m)t} + bA_{(n)t}) \qquad (2)$$
in years when spraying occurs.
- The maternal effects model does not explicitly include the larval stage. Rather, the initial larval density (prior to density-dependent larval mortality) is assumed to be proportional to the egg density. Therefore, the

Table 1: Comparison of model fits with and without an additional parameter for the effect of insecticide spraying on early larval stages following years of high pupal density.

Model		Culbin		Roseisle		Tentsmuir	
		LL	r^2	LL	r^2	LL	r^2
Maternal effects	Spray	1.45	0.64	0.80	0.49	0.83	0.60
	No Spray	1.44	0.64	0.80	0.49	0.83	0.60
Parasitoids	Spray	1.41	0.63	0.65	0.40	1.01	0.73
	No Spray	1.37	0.58	0.68	0.35	1.00	0.72
Food Quality	Spray	1.36	0.58	0.79	0.48	0.58	0.36
	No Spray	1.35	0.57	0.78	0.47	0.57	0.34

larval mortality due to spraying is imposed in Eq. (13), which becomes

$$A_{t+1} = r(1-\epsilon)E_{t+1}e^{-s(1-\epsilon)E_{t+1}+uW_t} \tag{3}$$

in years when spraying occurs (recall that spraying acts prior to larval density dependence). In the scaled version of the model this appears in the first line of Eq. (17), which becomes

$$N_{t+1} = r(1-\epsilon)N_t X_t e^{-s(1-\epsilon)N_t X_t + uX_t} \tag{4}$$

in years when spraying occurs. Similarly, the effect of egg density on weight (the second line of Eq. (17) presumably results from crowding in the larval stage, so the second line of (17) is replaced by

$$X_{t+1} = X_{\min} + e^{-\beta(1-\epsilon)N_t X_t} \tag{5}$$

when spraying occurs.

The results (Table 1) argue strongly against complicating the models by attempting to incorporate the effects of insecticidal spraying. Even given the rarity of spraying, it is surprising that the effects were so small. One possible explanation for this, suggested already by Crooke (1959), is that the outbreaks would have collapsed on their own in the absence of spraying. There were no control areas in Culbin that could be used to infer what would have occurred in the absence of spraying. However Crooke (1959) noted that other nearby forests "dropped rather sharply in density" (p. 190) and suggested that "Culbin could have been expected to behave in a somewhat similar fashion" (p. 190). In order to target the most vulnerable stages, spraying was timed to coincide with peak densities of early-instar larvae. Consequently, many of the individuals killed by spraying would have perished naturally due to the exceptionally intense larval crowding if spraying had not occurred.

As a final precaution we repeated the parametric bootstrap tests of constrained parasitoid models versus the maternal effects model, with spraying added to both models. The outcome was unchanged: for both Culbin and Tentsmuir, none of the bootstrap values (for the improvement in fit between maternal and parasitoid models) was as large as the value on the actual data.

Literature Cited

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