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Plume Continuity

Can threshold aggregation behavior produce an Allee effect in southern pine beetle populations?

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CONCEPT

Bark beetles use aggregation pheromones to locate susceptible hosts and to find mates.

An interruption in the aggregation signal results in a behavioral switch to emigration (Gara 1967; Billings 1980), promoting infestation failure.

Plume continuity is the uninterrupted maintenance of an aggregation signal over multiple generations of local infestation growth.

Overlapping generations are required for sustained infestation growth in multivoltine bark beetles (Fig. 1).

Many factors could potentially affect the probability of plume continuity. Here, we test three putative mechanisms: population size, stage structure, and predation on adults outside of hosts.

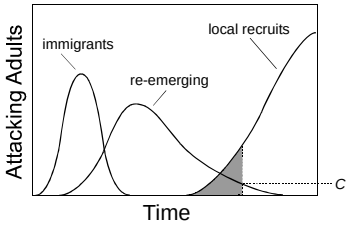

Figure 1. The concept of plume continuity. Adults immigrate into an aggregation, creating a pheromone plume. Re-emerging adults maintain the plume after immigration ends. Plume continuity is sustained if brood emerge before the parent generation drops below a critical threshold population size *C*. Below the threshold, the parent plume does not sustain aggregation, leading to brood emigration and infestation failure.

MODEL

Adults emerge, enter a host, and oviposit up to four times, laying 2.25 eggs per brood.

Offspring develop through egg, larva, pupa, and callow adult stages according to temperature-dependent rate curves modified from Gagne et al. (1982) and Wagner et al. (1984). Temperature regime obtained from Mississippi weather data.

How is the model novel? Individual variation is constant with regard to developmental rates, following the McKendrick-von Foerster framework (Gilbert et al. 2004; Powell and Logan 2005).

What did we manipulate?

Stage structure was implied by the synchronous spring emergence of adults. Synchrony should decrease the probability of plume continuity.

Predation was affected by decreasing the between-tree survival of emerging and re-emerging adults. Increased predation should decrease the probability of plume continuity.

Population size: the probability of plume continuity should increase with the number of individuals involved in infestation growth.

STAGE STRUCTURE

Result: Increased synchrony of adult emergence in the spring **decreased** the probability of plume continuity.

Synchrony was manipulated by changing the standard deviation (sigma) of emergence dates for the parent generation (Fig. 2).

Plume continuity was most sensitive to sigma when the number of colonizing adults was large (Fig 3).

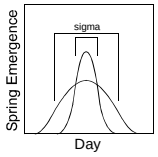

Figure 2. The relationship between sigma and the phenological synchrony of the parent population. A small value of sigma indicates a highly synchronous spring adult emergence.

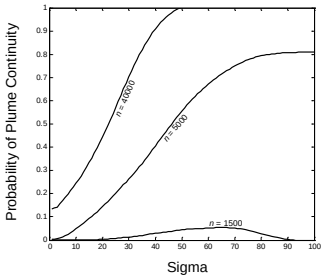

Figure 3. The probability of plume continuity as a function of sigma (SD of adult emergence date) and the size of the founding population (*n*). Between-tree survival = 0.5.

PREDATION

Result: Increased predation **decreased** the probability of plume continuity (Fig. 4).

By reducing average adult life span, predation shortens the duration over which **pheromone produced by re-emerged adults maintains aggregation behavior**.

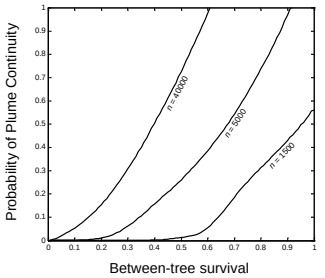

Figure 4. The probability of plume continuity as a function of increasing between-tree survival (reduced predation) and the size of the founding population (*n*). Sigma = 30.

AN ALLEE EFFECT

Result: For a given level of predation and phenological synchrony, the **probability of plume continuity increases with population size** at the scale of a forest (Fig. 5).

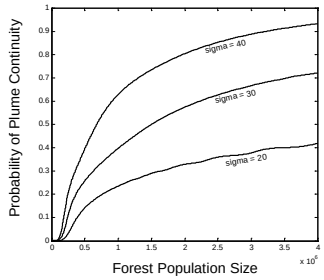

Figure 5. The probability of plume continuity as a function of population size and synchrony at the scale of a forest, assuming beetles initiate 100 local infestations with mean size *N*/100 and variance *N*. The high variance-to-mean ratio gives a slightly aggregated dispersion of beetles among spots. Between-tree survival = 0.5.

DISCUSSION

A seasonal departure from stable stage distribution should be advantageous for an organism which must mass-attack its host to overwhelm host defenses.

However, synchronous adult emergence in the spring leads to a decreased probability of plume continuity over the first generation of infestation growth.

Consequence?: Winters cold enough to synchronize a population (*sensu* Powell et al. 2000) may be followed by a high rate of infestation failure in the spring. Plume continuity may also be disrupted by high summer temperatures via brood mortality (Beale 1931) or delayed emergence (R. Billings, personal observation).

Plume continuity is more likely if predation is low.

Consequence?: predation on southern pine beetle by its specialist clerid predator may contribute to infestation failure by reducing the average life span of adults.

Threshold aggregation behavior in southern pine beetles can lead to an Allee effect at the scale of whole forests.

Consequence?: an Allee effect can modulate the transition between endemic and epidemic states in outbreak pests (Berryman 1986).

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