

Evolutionary Ecology of Pheromone Signaling in *Dendroctonus frontalis*

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Although studies of pheromone production in the southern pine beetle (*Dendroctonus frontalis*) extend back to the dawn of chemical ecology, it is only recently that instrumentation has become sufficiently sensitive to measure pheromone production of individual beetles. Now, recent studies have revealed surprisingly high variation among individuals in their pheromone production. This seems paradoxical because pheromone signals in tree-killing bark beetles are apparently linked to fitness and have high heritability. We tested whether variation has been overestimated by hindgut extractions, which can only measure static pools of pheromones; but variation among individuals was similarly high for life time production of pheromones via individual aerations (CV = 60 to 182 percent). An alternative hypothesis is that natural selection is constrained by the aggregation behavior of *D. frontalis*. In fact, the phenotypic trait visible to selection is the pheromone plume emanating from a tree, which is the collective property of all the beetles in the group. We evaluated the effect of individual beetles on the pheromone plume by using the empirical frequency distributions of pheromone production to analyze simulated aggregations with variable group sizes. For realistic aggregation sizes of 300 to 1,300 females per meter of host tree, the average effect of a beetle on the plume was very low (generally < 10 percent). By application of Fisher's Fundamental Theorem of Natural Selection, this represents the maximum opportunity for selection on individual pheromone production (assuming that heritability is perfect and the pheromone plume is the sole determinant of fitness). We conclude that pheromone production is a nearly neutral trait in *D. frontalis* because individuals have only very minor effects on the phenotypic trait under selection (the pheromone plume). Therefore, genetic variation accumulates via mutation and recombination, unchecked by natural selection, even though pheromone production is highly heritable and properties of the pheromone plume have generally strong effects on the fitness of individuals within the aggregation.

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