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In Population Dynamics, It's a Dogma Eat Dogma World

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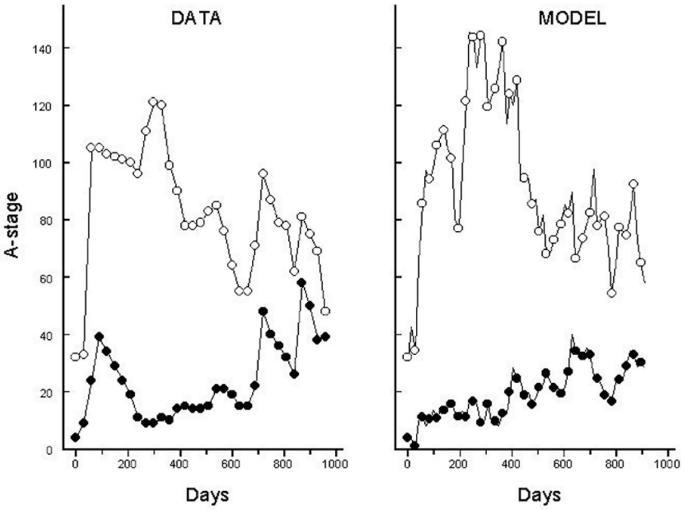

Flour Power. In a classic paper published in 1968, Thomas Park and colleagues noted the anomalous coexistence of two species of flour beetles over a period of nearly three years: T. confusum *(open circles) and* T. castaneum *(solid circles) both thrived for 960 days (left). Analysis of a new mathematical model suggests that the anomaly was no accident (right).*

Genus *Tribolium*—the lowly flour beetle—is a pest. Leave a bag of flour long enough, and you're likely to find it crawling with the critter, whose life cycle proceeds from egg to larva to pupa to egg-laying adult. Now *Tribolium*—or, more exactly, a team of biologists and mathematicians studying the flour beetle—is threatening one of the long-held tenets of population dynamics: the notion that two similar species competing for the same limited resource cannot coexist.

The flour beetle team includes biologists Bob Costantino, now at the University of Arizona, Robert Desharnier of California State University at Los Angeles, and Aaron King of the University of Tennessee; statistician Brian Dennis of the University of Idaho; and mathematicians Jim Cushing of the University of Arizona, Shandelle Henson of Andrews University in Berrien Springs, Michigan, and Jeff Edmunds of Mary Washington College in Fredericksburg, Virginia. In 1997, the team (minus Henson and Edmunds) reported the first experimental evidence of chaos in an actual population (see "Chaotic Bugs Make the Leap from Theory to Experiment," *SIAM News*, July/August 1997). After developing a mathematical model that accurately describes a "control" population of the species *T. castaneum*, they artificially manipulated the beetles' mortality rate to verify the predictive power of the model. In particular, they showed that the period-doubling route to chaos exhibited by their laboratory populations is the same as that seen in the equations.

The new results, which will appear in the *Journal of Animal Ecology*, are, for now, purely mathematical, but they point the way to experiments the team intends to do. The beetle researchers have found that, according to their model, two species can get along just fine, even though (or possibly because) they fight like mad. This "flies right in the face of classical competition dogma," Cushing says. It violates a tenet of ecology known as the "prin-ciple of competitive exclusion."

Survival of the Fittest—or Luckiest

The principle of competitive exclusion asserts that when two similar species compete for the same resource, one of them invariably dies out. It's one of the central tenets of ecology, Costantino says. "Every introductory course in the country teaches it. We hope we will shake it just a little."

Somewhat more precisely, the principle of competitive exclusion does allow for coexistence, if the competition between the species is weak. Beyond some threshold, however, the coexistence state (along with the initial conditions drawn to it) becomes unstable; in this case, it serves only as a boundary between two basins of attraction that correspond to the two possible extinctions. (If there's a strong asymmetry between the species, the coexistence state may disappear altogether, leaving just one result.) The standard models of population dynamics, generically known as Lotka–Volterra models, all adhere to this seemingly common-sense picture of a ruthless world.

So did some classic flour beetle experiments of the 1950s and 60s. Thomas Park, whom Costantino calls the "father" of flour beetles, did a series of experiments with *T. castaneum* and *T. confusum*. He established that the two species do indeed compete, and in his experiments one species almost always drove the other to extinction. In 1968, Park and colleagues Patrick Leslie and David Mertz reported on a set of experiments in which they started with bottles containing the 25 combinations of 4, 8, 16, 32, and 64 adults of each of the two species; censusing was done at 30-day intervals. The resulting time series conformed to the principle of competitive exclusion.

With one exception. The trial that began with 4 *castaneum* and 32 *confusum* ran for 960 days (32 data points), with no indication that either species was winning the beetle bottle battle. Park et al. had no explanation for the anomaly, although they speculated that they were simply witnessing an extremely long transient. (They interrupted the experiment to test whether there had been some change in the beetles themselves during their two-and-a-half-year power struggle. None was found.)

Indeed, the mathematical model they used—a discrete-time stochastic model developed by Leslie and John Gower—supported the long-transient possibility. According to the Leslie–Gower model, if the numbers of adults of the two species at (census) time t are A_t and A'_t, respectively, then the expected numbers of adults at time $t + 1$ are

$$\begin{aligned} A_{t+1} &= rA_t/(1 + aA_t + bA'_t) \\ A'_{t+1} &= r'A'_t\,(1 + a'A'_t + b'A_t), \end{aligned}$$

where r, r', a, a', b, and b' are positive parameters. (The stochastic part of the model is too technical to go into here.) Park's group used values $r = 1.7507$, $r' = 1.6854$, $a = 0.008435$, $a' = 0.004129$, $b = 0.009734$, and $b' = 0.042983$. In the deterministic Leslie–Gower equations, the species driven to extinction switches from *castaneum* to *confusum* when the initial populations go from (4,32) to (5,31), indicating proximity to an initial population that will head to a coexisting equilibrium, in this case near (9,69). However, the stability of the equilibrium depends on the ratio bb'/aa', which in this case is about 12; because it is considerably larger than 1, this ratio indicates that the equilibrium is highly unstable.

In the stochastic setting, the model drove *castaneum* to extinction about a third of the time when starting at (4,32). Reassuringly, the Monte Carlo simulations (all 60 runs—remember, this work was done in the age of mainframes, when people got billed for computer time) indicated an average time to extinction of 1120 days, with a standard deviation of about 350 days. It's too bad Park and colleagues didn't let the lab experiment keep going, Costantino says. In effect, the anomalous result was duly noted, reported, published, and forgotten.

Till now.

Let Us Prey Together

In 1999, Cushing assigned his graduate student Jeff Edmunds the job of analyzing the dynamics of two interacting copies of the beetle team's LPA model, which they had developed for their earlier chaos experiments. The LPA model is markedly different from the Leslie–Gower model. In particular, it keeps track of three life stages: larva, pupa, and adult (hence the acronym). The basic equations are

$$\begin{aligned} L_{t+1} &= BA_t \exp(-(c_{EL}L_t + c_{EA}A_t)/V) \\ P_{t+1} &= (1 - r_L)L_t \\ A_{t+1} &= P_t \exp(-c_{PA}A_t/V) + (1 - r_A)A_t, \end{aligned}$$

where the key nonlinearities are governed by the "cannibalism coefficients" c_{EL}, c_{EA}, and c_{PA}, representing the feasting on eggs by larvae and on eggs and pupae by adults. The parameters B, r_L, and r_A represent birth and death rates in the absence of cannibalism. The mathematically extraneous V represents the volume of flour the beetles are raised on; the beetle team does its experiments with 20 grams, which is refreshed every two weeks, when Costantino counts the beetles. The two-week cycle, another difference from the earlier work, was chosen because of a convenient feature of the flour beetle's life cycle: The average beetle spends two weeks as a larva and two weeks as a pupa, so that a biweekly census gives a pretty good snapshot. (On the other hand, it's a lot of biweekly work for Costantino, who does all the counting himself. It takes him only about 45 minutes to count a beetle population, but at any given time he has upward of 40 populations to count. "Bob just loves this kind of detailed work," Cushing says. "He gets a twinkle in his eye!")

When two species are put together, the number of parameters in the LPA model jumps to 18: the six cannibalism coefficients and birth and death rates for each species separately, and six more cannibalism coefficients representing the predation by larvae and adults of each species on the eggs and pupae of the *other* species. That's a lot of parameters to vary, so Edmunds began by fixing most of them, using rounded values in the range that the beetle team had estimated from their experiments with *T. castaneum*. Using upper- and lowercase letters for the two species, he wound up setting $b = B = 10$, $r_l = r_L = 0.2$, $r_a = r_A = 0.02$, $c_{el} = c_{EL} = c_{eL} = c_{El} = 0.01$, $c_{ea} = c_{EA} = c_{eA} = c_{Ea} = 0.01$, and $V = 0.4$.

In this slice of parameter space, Edmunds showed that the beetles would be drawn to a coexisting equilibrium when the interspecies pupa-feasting was relatively weak. The beetle team settled on values $c_{Pa} = 0.005$, $c_{pA} = 0.008$, $c_{pa} = 0.01$, and $c_{PA} = 0.012$ (meaning that the uppercase beetles are slightly more voracious than the lowercase cousins). With these values, it's not hard to show that the two populations tend to $(L,P,A) = (17.6, 14.1, 61.1)$ and $(l,p,a) = (14.1, 11.3, 48.9)$. (With other parameters equal for the two species, the equilibrium is characterized by the ratios $l/L = p/P = a/A = (c_{PA} - c_{pA})/(c_{pa} - c_{Pa})$, which in this case equals 0.8. The larval death rate $r_L = 0.2$ implies $p = 0.8l$, which explains why $P = l$.

So far, this is all perfectly consistent with the principle of competitive exclusion, which predicts coexistence (and not extinction) when the competition is weak. But Edmunds wasn't done.

"One of the things I told Jeff to do was to keep his eye open for any unusual dynamics," Cushing recalls. So Edmunds started looking at birfurcations as he varied some of the other parameters. He got striking results.

In particular, Edmunds looked at what happens when the interspecies egg-eating by larvae increases—that is, when the parameters c_{eL} and c_{El} go up. Fixing the other parameters as before and increasing these two numbers in tandem, he found that the coexistence equilibrium slowly erodes, with the uppercase species (which the beetle team calls *T. castaneum*) becoming increasingly dominant, until it is replaced by extinction of the lowercase species (*T. confusum*) at around $c_{eL} = c_{El} = 0.02$.

This is still in keeping with the principle of competitive exclusion. The first glimpse of something strange occurs at about 0.024. There, the stable extinction of *T. confusum* is joined by a stable equilibrium in which *T. confusum* predominates over *T. castaneum*.

The predominance of *T. confusum* in this equilibrium increases up to about 0.025, at which point *T. castaneum* goes extinct. From there to about 0.029, the principle of competitive exclusion is back in business, with two stable extinctions and no stable coexistence solutions. (A second, unstable equilbrium and an unstable 2-cycle appear at the same time as the stable equilibrium and persist for higher values of the parameter.)

The most interesting dynamics emerges at around 0.029, with the appearance of a stable 2-cycle. From there on, there are three stable solutions: the two extinctions and this unusual, principle-of-competitive-exclusion-defying, coexistence state. Moreover, the stable 2-cycle in the region above 0.029 causes long transients before extinction in the region below 0.029—so the speculation of Park et al. about the likely fate of their (4,32) beetles could have been right for reasons they could not have known.

Back to the Lab

It remains to be seen, of course, whether any of the newfound dynamics occurs in actual flour beetle populations. "We're gearing up to do the experiments," Costantino says. The first step is to validate the LPA model for a second species. Then it will be necessary to estimate the interspecies cannibalism coefficients. One of the challenges will be figuring out how to manipulate the competition parameters in the laboratory. (In the earlier chaos experiments, it was fairly easy to manipulate the adult death rate.) Designing the experiments—in particular, deciding which combinations of initial populations to try—will require close study of the mathematical model.

There's more to be done mathematically as well. Cushing and a current grad student, Sheree Levarge, have analyzed the Leslie–Gower model and proved that it never violates the principle of competitive exclusion. Some sort of multistage life cycle may be necessary for stable coexistence to appear alongside extinction—the 2-cycle makes sense in that the egg-eating larvae are voracious enough that a large number in one generation will depress the number born to the next, thus allowing the number to rebound in the second generation—but two stages may suffice. Cushing and Henson have in fact found the same dynamics in a (theoretical) system in which one "species" goes through two stages and the other only one.

The beetle team is also looking at stochastic aspects of their model. Another question is what happens when the models take into account the fact that real beetle populations are counted in non-negative integers, not real numbers. These two issues are probably best combined, Cushing points out: Deterministic dynamics on a (small) finite lattice quickly becomes cyclic, for obvious reasons; a random component restores the analytic complexity.

Asked for an assessment of the beetle team's progress in attacking problems in flour beetle dynamics, Cushing can't resist an analogy. "I'd say we're in the larval stage," he says. "It's the most voracious!"

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