Park's *Tribolium* competition experiments: a non-equilibrium species coexistence hypothesis

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Summary

1. In this journal 35 years ago, P. H. Leslie, T. Park and D. B. Mertz reported competitive exclusion data for two *Tribolium* species. It is less well-known that they also reported 'difficult to interpret' coexistence data. We suggest that the species exclusion and the species coexistence are consequences of a stable coexistence two-cycle in the presence of two stable competitive exclusion equilibria.

2. A stage-structured insect population model for two interacting species forecasts that as interspecific interaction is increased there occurs a sequence of dynamic changes (bifurcations) in which the classic Lotka–Volterra-type scenario with two stable competitive exclusion equilibria is altered abruptly to a novel scenario with three locally stable entities; namely, two competitive exclusion equilibria and a stable coexistence cycle. This scenario is novel in that it predicts the competitive coexistence of two nearly identical species on a single limiting resource and does so under circumstances of increased interspecific competition. This prediction is in contradiction to classical tenets of competition theory.

Key-words: competitive coexistence, competitive exclusion, flour beetle, Thomas Park.

Journal of Animal Ecology (2003) **72**, 703–712

Introduction

Thomas Park (1948) deliberately chose two closely related species, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst, for his long-term study of interspecies competition. Park found support for using related species in a comment by Darwin (1859: Chapter III), 'As the species of the same genus usually have, though by no means invariably, much similarity in habitats and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera.' In three different experiments Park (1948, 1954, 1957) found that one of the two species always became extinct.

During the years following Park's experiments, when the theories of competitive exclusion and ecological niche were being debated, many researchers studied Park's 1954 data carefully (Costantino & Desharnais 1991). The main conclusion from these studies was that Park's experimental results supported the tenet that two nearly identical species cannot coexist on a single

coexist when exploiting a shared habitat in the laboratory … This, now rather hoary, conclusion runs the risk of becoming dogma. Indeed, it would be quite an exciting counterirritant if exceptions, derived from careful study and meaningful design, could be found.' Park continued his study of this question in a later experiment. Eight genetic strains were developed to further examine competition. Following very extensive competition experiments with these genetic strains Park, Leslie & Mertz (1964: 150) wrote, 'It is true that one species always excluded the other when these particular strains were competing together. But, if we accept the logical consequences of the way two species may be interrelated in terms of the model, it would follow that other strains of the two *Tribolium* might in time be found, which would exhibit the phenomenon of coexistence of both species in a competitive system. Theoretically speaking, the so called Gause's Principle does not necessarily hold in all possible cases.' It is clear that Park was still not convinced that coexistence was unattainable.

Park's final experiment (Leslie, Park & Mertz 1968), concluding a 20-year programme on species competition, can be summarized as follows: in 24 of a total of 25 mixed species cultures one or the other of the species went extinct. There was, however, a glaring exception. In one culture the two species coexisted for 960 days (over 30 generations). From a theoretical viewpoint, the outcome of the experiment is consistent with a system in which there is stable coexistence together with two stable, competitive exclusion equilibria, i.e. some initial conditions lead to the extinction of *T. castaneum*, other initial conditions to the extinction of *T. confusum* and still others lead to species coexistence. In the context of the classical two-species Lotka–Volterra model this dynamic scenario is not possible. Leslie *et al.* (1968) were unable to explain these observations satisfactorily and concluded, seemingly reluctantly, that coexistence was not observed. We would like to suggest another hypothesis to explain these data – a hypothesis that includes the coexistence of the two beetle species.

Our paper is organized as follows. We begin with a review of the experimental protocol and the results of the competition experiment conducted by Leslie *et al.* (1968). The time–series data of the culture in which the two *Tribolium* species coexisted for 960 days will be the central focus of our analysis. Next we describe how a well-validated discrete, non-linear stage-structured model for flour beetles (Cushing *et al.* 2003) can be extended to include two interacting species (Edmunds 2001). From this two-species model we will establish a multiple attractor, coexistence hypothesis of non-

where N_t and M_t are the number of adults of species 1 and 2 at time t, respectively, and λ_1, λ_2, α_1, α_2, β_1, β_2 are positive constants, provides theoretical predictions for the long-term outcome of the competitive interaction. This 'Leslie–Gower model', all of whose orbits asymptotically approach an equilibrium, provides (when λ_1 and $\lambda_2 > 1$) only three dynamic scenarios, the same three possibilities associated with the well-known Lotka–Volterra competition model. If interspecies competition is sufficiently strong ($\beta_1 > \alpha_2(\lambda_1 - 1)/(\lambda_2 - 1)$ and $\beta_2 > \alpha_1(\lambda_2 - 1)/(\lambda_1 - 1)$), then orbits approach an equilibrium in which one species is absent. The later case occurs in two fundamentally different ways that depend on the values of the model parameters: either all initial states of the two populations approach asymptotically the same competitive exclusion equilibrium (so that the same species is always eliminated) or the final competitive exclusion state depends on the initial states (so that which species is eliminated depends on the initial states). The second case is distinguished by the existence of a coexistence equilibrium which, however, is unstable. This equilibrium is a 'saddle' and there is a one-dimensional 'stable manifold' of orbits that approach it. This manifold forms a boundary

With parameters estimated from the data, the Leslie–Gower model predicts an unstable coexistence (saddle) equilibrium (Leslie *et al.* 1968: 11). Thus, some initial conditions lead to the extinction of *T. castaneum* and others to the extinction of *T. confusum*. As a result, the model does not provide an explanation for the possible species coexistence observed in Fig. 1.

Leslie *et al.* (1968: 23) fully appreciated not only the role of models in their ecological research but also the powerful future role of connecting data to biologically based mathematical models:

> Despite the simplicity of the assumptions involved, the model has proved an invaluable interpretative aid and has even been predictive over a wide range of *Tribolium* experiments involving different genetic

as cannibalizing its own. For example, the coefficient c_{eL} represents the consumption of species 1's eggs by the larvae of species 2, c_{El} represents the consumption of species 2's eggs by the larvae of species 1, and c_{el} and c_{EL} are the intraspecific cannibalism coefficients. The other cannibalism coefficients are interpreted in similar fashion. The model has 12 competition coefficients in all: six intraspecific coefficients and six interspecific coefficients.

Results

We want to emphasize that the parameter values we use are consistent with the biology of the flour beetle; however, we did not fit the LPA model statistically to the adult time–series data reported by Leslie *et al.* (1968). Indeed, those data are inadequate for that purpose. Our interest is to examine the dynamics of one of Park's classic *Tribolium* experiments using the two-species LPA model with biologically reasonable parameters. We let 'species 1' (represented by lower-case letters) be *T. confusum* and 'species 2' (given by upper-case letters) be *T. castaneum*.

In the experiment reported by Leslie *et al.* (1968), the habitat size was 8 g. Because the habitat size V in the LPA model is expressed in units equal to the volume occupied by 20 g of standard medium, we set $V = 8/20 = 0.4$. For the other parameter values we use rounded values in the range of the parameters estimated from recent laboratory experiments with *T. castaneum* cultured in a 20-g habitat (Dennis *et al.* 2001): $b = B = 10$, $\mu_l = \mu_L = 0.2$, $\mu_a = \mu_A = 0.02$, $c_{el} = c_{EL} = c_{El} = c_{eL} = 0.01$, $c_{ea} = c_{EA} = c_{Ea} = c_{eA} = 0.01$. With these parameter values, a positive equilibrium exists when interspecific competition represented by c_{Pa} and c_{pA} is less than intraspecific competition represented by c_{pa} and c_{PA} (Edmunds 2001). Inequalities such as $c_{Pa} < c_{pA} < c_{pa} < c_{PA}$ are sufficient (but not necessary). We use the parameters $c_{Pa} = 0.005$, $c_{pA} = 0.008$, $c_{pa} = 0.01$ and $c_{PA} = 0.012$.

The bifurcation diagram presented in Fig. 2 is a summary of the dynamics of the two species system as the interspecific coefficients c_{eL} and c_{El} change simultaneously from 0·016 to 0·032 with all other parameters held constant. There are five distinct regions in the figure which we denote by the letters A, B, C, D and E. We now discuss the general dynamic features of each region. The graphs in Fig. 3 present projected phase space depictions of representative model orbits in each of the five different regions.

Regions A and B contain classical Lotka–Volterra dynamic scenarios. In region A there is a globally attracting coexistence equilibrium. In region B there is a globally stable competitive exclusion equilibrium, implying persistence of *T. castaneum* and the extinction of *T. confusum*.

In region C there is a stable positive equilibrium which exists in the presence of a stable exclusion equilibrium. This is an unusual, non-Lotka–Volterra scenario. However, these dynamics exist for only a small range of parameters. Certain initial conditions for which *T. confusum* has a significant advantage result in coexistence. Other initial conditions lead to the extinction of *T. confusum* and an equilibrium for *T. castaneum*.

In region D there are two competitive exclusion equilibria, with some initial conditions leading to the extinction of *T. confusum* and others leading to the extinction of *T. castaneum*. The coexistence equilibrium is an unstable saddle. This is a classical Lotka–Volterra ous9u3(band others leading to th(.)eum)Tj /F2 1 T
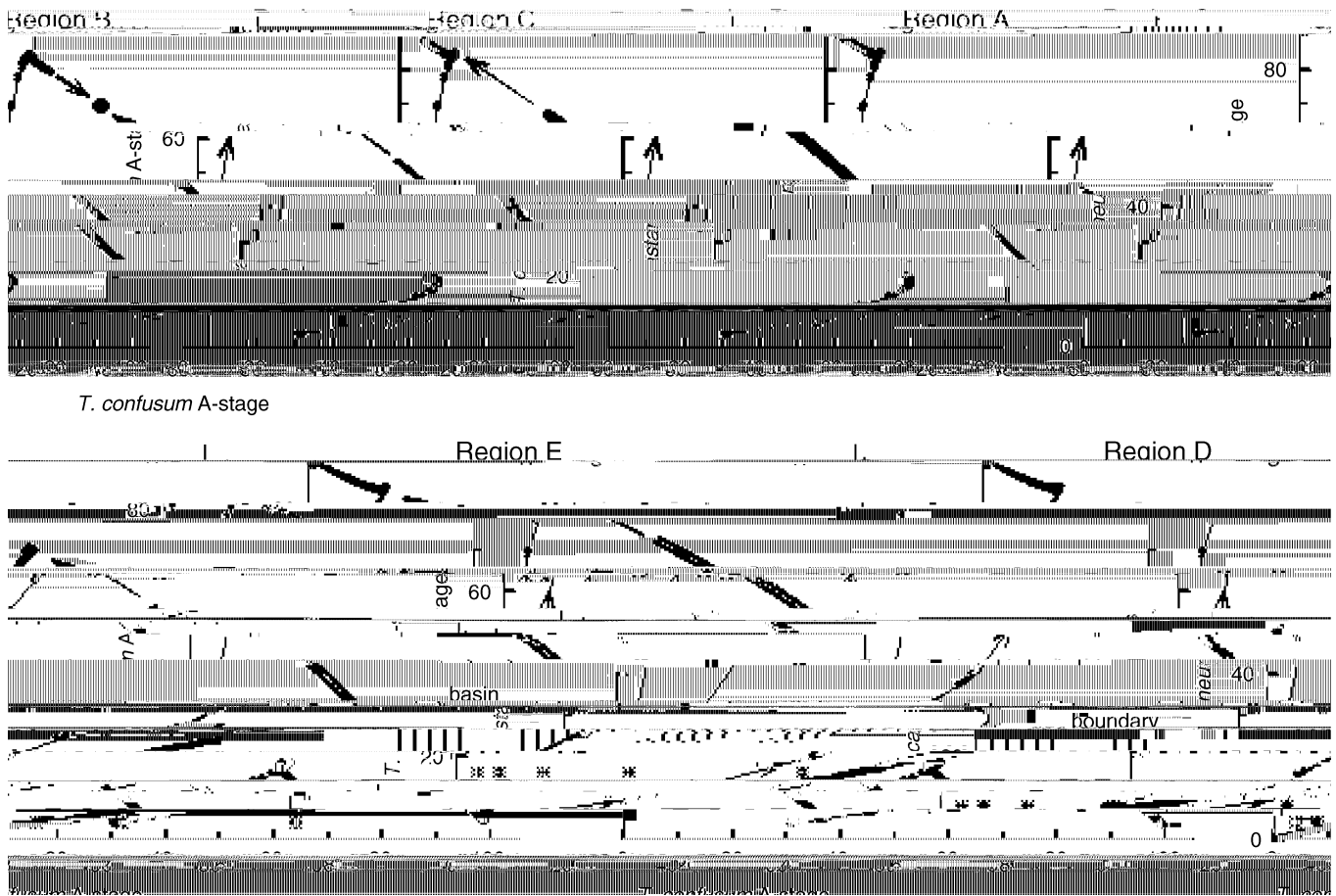
T. confusum A-stage

Fig. 3. Phase space graphs of representative deterministic LPA model orbits for the regions A, B, C, D and E given in Fig. 2. Region A, $c_{eL} = c_{El} = 0.018$: classical Lotka–Volterra type dynamics with a globally attracting equilibrium; all positive initial conditions result in equilibrium coexistence. Region B, $c_{eL} = c_{El} = 0.022$: classical Lotka–Volterra type dynamics with a globally attracting axis equilibrium; all positive initial conditions result in the extinction of *T. confusum* and an equilibrium state for *T. castaneum*. Region C, $c_{eL} = c_{El} = 0.0244$: non-classical Lotka–Volterra-type dynamics. A saddle node bifurcation gives rise to a stable coexistence equilibrium which exists in the presence of a stable axis equilibrium. Some initial conditions result in coexistence, while others lead to the extinction of *T. confusum* and an equilibrium state for *T. castaneum*. Region D, $c_{eL} = c_{El} = 0.028$: classical Lotka–Volterra-type dynamics with two stable axis equilibria and an unstable coexistence equilibrium. Together with Leslie *et al.* (1968), we use this hypothesis to explain the outcomes of their 1968 experiment. The basin boundary separates initial conditions which result in the extinction of *T. castaneum* from those which result in the extinction of *T. confusum*. Asterisks denote those initial conditions used in the 1968 Leslie experiment. Region E, $c_{eL} = c_{El} = 0.032$: non-classical Lotka–Volterra dynamics. A saddle-node bifurcation of the composite map gives rise to a stable, positive two-cycle wi
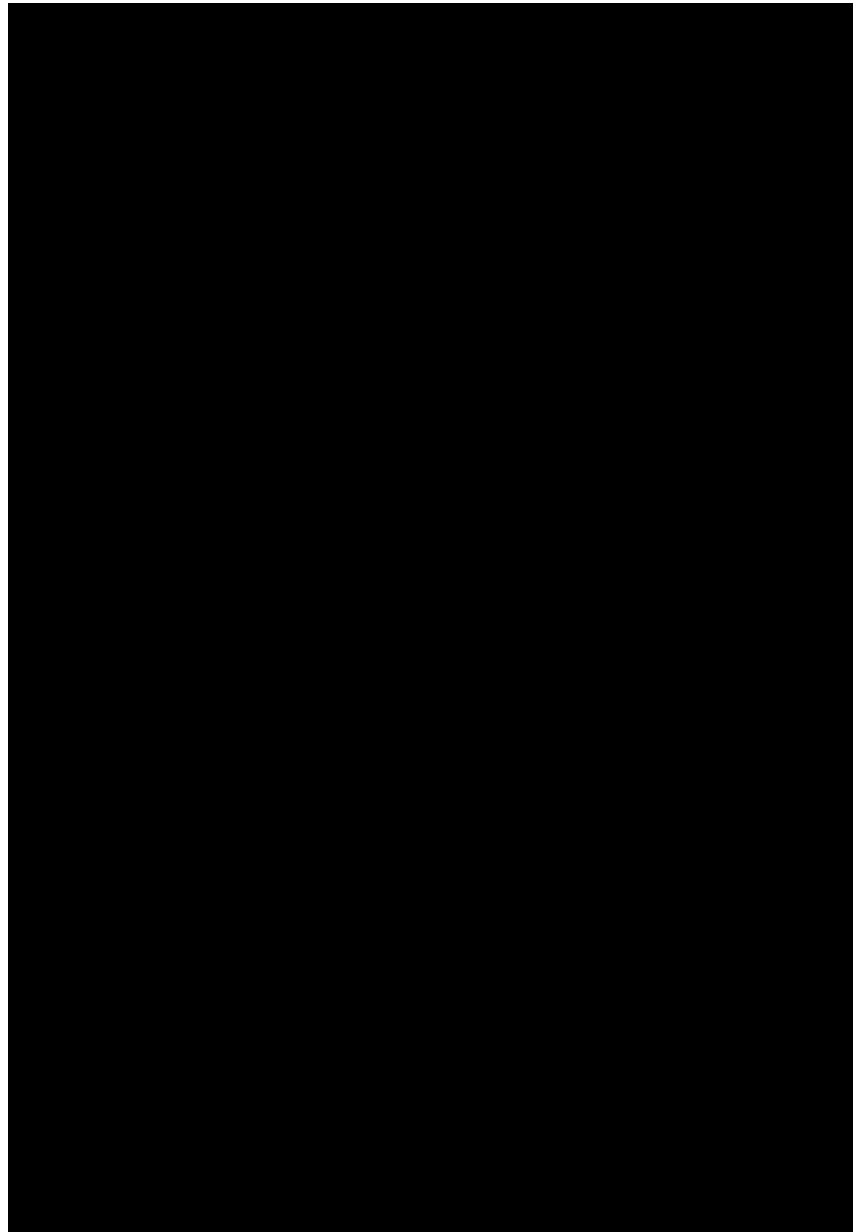
scenarios allow (asymptotically) only equilibrium dynamics and, when interspecific competition is sufficiently severe, only one surviving species. An example is the Leslie–Gower model that was applied to the historic *Tribolium* experiments of Park. Under more general assumptions, however, the outcomes predicted by theoretical competition models are not always so limited and do not necessarily support the classical competitive exclusion principle (Koch 1974; McGehee & Armstrong 1977; Levins 1979; Cushing 1980; de Mottoni & Schiaffino 1981; Cushing 1983; Waltman 1983; Cushing & Saleem 1984; Namba 1984; Chesson 1985; Cushing 1986; Namba 1986; Freedman *et al.* 1989; Crowe 1991; Namba & Takahashi 1993; Loreau & Ebenhoh 1994; Smith & Waltman 1995; Cushing 1998; Huisman & Weissing 1999, 2001; Li 2001). These theoretical results are not known widely to ecologists, perhaps because they have never been tied to any specific biological examples or data. Unlike the competition LPA model, however, we know of no theoretical model that predicts the simultaneous occurrence of both coexistence and exclusion attractors.

A notable feature of the theoretical models that contradict the classical competitive exclusion principle is

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