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

JEFFREY EDMUNDS*, J. M. CUSHING†, R. F. COSTANTINO‡, SHANDELLE M. HENSON§, BRIAN DENNIS¶ and R. A. DESHARNAIS**

**Department of Mathematics, Mary Washington College, Fredericksburg, VA, 22401; †Department of Mathematics, Interdisciplinary Program in Applied Mathematics, University of Arizona, Tucson, AZ, 85721; ‡Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, 85721, §Department of Mathematics, Andrews University, Berrien Springs, MI 49104; ¶epartment of Fish and Wildlife Resources and Division of Statistics, University of Idaho, Moscow, ID, 83844; and **Department of Biological Sciences, California State University, Los Angeles, CA, 90032, USA*

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.

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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 limiting resource. In these studies the beetle experiments were interpreted in terms of the classical Lotka–Volterra scenario in which the coexistence equilibrium is unstable and two competitive exclusion equilibria are stable. In this scenario one or the other species survives, depending on initial population numbers, and coexistence is not possible. As a result of this interpretation, the beetle competition experiments (Park 1948, 1954, 1957) have often been invoked in support of the fundamental principles of competitive exclusion, limiting similarity and ecological niche (Gause 1934; Cole 1960; Hardin 1960; May 1974).

Park was not completely convinced, however, that *Tribolium* species could not coexist. He wrote (Park 1957: 35), 'The general conclusion is that these two species, rather similar to each other in their ecology, do not

Correspondence: Jeffrey Edmunds, Department of Mathematics, Mary Washington College, Fredericksburg, VA 22401, USA. E-mail: jedmunds@mwc.edu

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-Lotka–Volterra type. Finally, using this hypothesis, we will propose an explanation of both species exclusion and species coexistence observed by Leslie *et al.* (1968).

LESLIE–PARK–MERTZ EXPERIMENT

We state briefly the laboratory protocol of the Leslie *et al.* (1968) experiment. Full details are given in the original publication. Populations initiated in all combinations of 0, 4, 8, 16, 32 and 64 adults of *T. castaneum* cIV-a and *T. confusum* bI were cultured in shell vials with 8 g of standard medium and maintained in an incubator at 29 °C, 70% relative humidity. The populations were censused at 30-day intervals at which time the medium was changed. Only the adult stage was counted. All life stages (eggs, larvae, pupae and adults) were returned to fresh medium. The experiment ended after the census taken on day 960.

The time–series data of the 'coexistence' culture, which was initiated with four adults of *T. castaneum* and 32 adults of *T. confusum*, are given in the top panel of Fig. 1. The time–series data for a culture started with eight adults of *T. castaneum* and 64 adults of *T. confusum* are given in the bottom panel. We quote the description of these data (referred to as systems A and B) given by Leslie *et al.* (1968: 18):

> The initial rise in adult numbers of both species was followed as usual by a gradual fall until, by day 270, there were less than 10 adult cIV-a surviving, compared with more than 100 adult bI. At this point, one might have expected the numbers of cIV-a to continue to decrease until this species became extinct. This expected elimination of *T. castaneum* occurred on day 510 in systems B and C; but the subsequent course of events after day 270 in system A was very different.
>
> Instead of disappearing, the numbers of adult cIV-a remained at a fairly steady level of some 10–21 individuals for nearly a year, between days 330 and 660, during which the numbers of bI slowly decreased from 120 to 55 adult individuals. At this point it appeared as though the latter strain would gradually be eliminated, although its adult age-groups were probably still being recruited by a certain number of emergences from the pupal stage, as indicated by the continued presence of small numbers of 'callow' bI dead. The events after day 660, however, were rather difficult to interpret. During this last period of nearly a year in the history of this system, there were two sudden rises in the adult numbers of both species, which occurred more or less simultaneously, the peak numbers in both cases being reached on days 720 and 870. Given the known voracious cannibalism of this *T. castaneum* strain, the effect of which had been so manifest in the other systems in this experiment, it was difficult to understand why these sudden rises in adult numbers of bI should have occurred at times when the numbers of *T. castaneum* seemed sufficiently high to prevent any such relatively massive recruitments of the adult bI population from taking place.

To study these data Leslie *et al.* (1968) used a discrete-time stochastic model for two species proposed a decade earlier by Leslie & Gower (1958). The deterministic model,

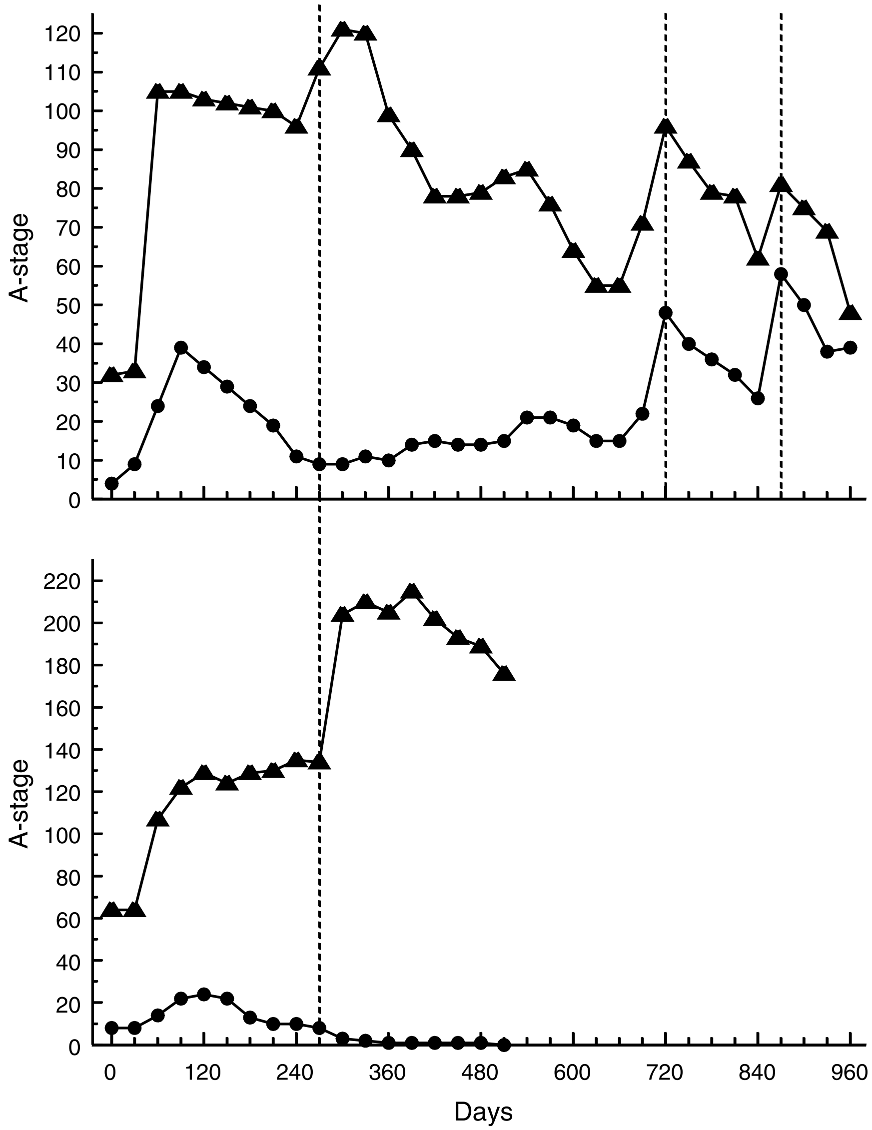

Fig. 1. Adult time–series for two cultures in the Leslie *et al.* (1968) experiment. In the top panel a culture started with four adults of *T. castaneum* strain cIV-a (circles) and 32 adults of *T. confusum* strain bI (triangles). In the bottom panel a culture started with eight adults of *T. castaneum* strain cIV-a (circles) and 64 adults of *T. confusum* strain bI (triangles).

$$N_{t+1} = \frac{\lambda_1 N_t}{1 + \alpha_1 N_t + \beta_1 M_t}$$

$$M_{t+1} = \frac{\lambda_2 M_t}{1 + \alpha_2 M_t + \beta_2 N_t}$$

where N_t and M_t are the number of adults of species 1 and 2 at time *t*, respectively, and $\lambda_1, \lambda_2, \alpha_1, \alpha_2, \beta_1, \beta_2$ 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 that separates initial conditions that approach the different competitive exclusion equilibria. The third possibility occurs when interspecies competition is sufficiently weak ($\beta_1 < \alpha_2(\lambda_1 - 1)/(\lambda_2 - 1)$ and $\beta_2 < \alpha_1(\lambda_2 - 1)/(\lambda_1 - 1)$) and all initial states approach a coexistence equilibrium in which both species are present.

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 strains which possess differing competitive mechanisms. We do not understand why the model should be so successful but the fact of our success suggests that experimentally we are dealing with a set of interlocking biological mechanisms, nearly all of which are reconcilable (at least as a first approximation) with the structure and resulting properties of the model itself. We consider that this wedding of theory with fact has added a new, though preliminary, dimension to the understanding of ecological phenomena; and we believe that this type of approach will prove to be even more rewarding in the future.

We continue in the tradition set by Leslie, Park and Mertz with the introduction of a new two-species model applied to *Tribolium*.

LPA *TRIBOLIUM* MODEL

The Leslie–Gower model has several shortcomings for describing the interaction between two species of *Tribolium*. In the experiment only the adults of each species were counted, so a model with only adults seemed to them to be an asset; nevertheless, the model formulation does not identify specifically the important interspecific and intraspecific interactions occurring among the different life stages. Because the primary source of interaction in these species is cannibalism of eggs by larvae and adults and of pupae by adults, an effective model must consider the individual life stages as separate entities. However, cannibalism was not acknowledged fully as the primary mechanism responsible for the species interaction in *Tribolium* until 1970 (Park *et al.* 1970). Another limitation of the Leslie–Gower formulation is that the long-term behaviour of the population will always be an equilibrium state, whether or not the species coexist. In fact, *Tribolium* populations often oscillate. As discussed above, the dynamic possibilities provided by the Leslie–Gower model are identical to those of the Lotka–Volterra model.

The LPA model is a system of three discrete time difference equations that relate the numbers of larvae, pupae and adults at time t to the numbers in these stage-classes at time $t + 1$:

$$L_{t+1} = BA_t \exp\left(-\frac{c_{EL}}{V}L_t - \frac{c_{EA}}{V}A_t\right)$$

$$P_{t+1} = (1 - \mu_L)L_t$$

$$A_{t+1} = P_t \exp\left(-\frac{c_{PA}}{V}A_t\right) + (1 - \mu_A)A_t.$$

Here L_t, P_t and A_t are, respectively, the number of feeding larvae, the number of non-feeding larvae, pupae and callow adults, and the number of sexually mature adults at time t. The unit of time is 2 weeks, which is the approximate amount of time spent in each of the L and P classes under experimental conditions. $B > 0$ is the average number of larvae recruited per adult per unit time in the absence of cannibalism, and the fractions μ_A and μ_L are the adult and larval probabilities of dying from causes other than cannibalism in one time unit. The exponentials represent the fractions of individuals surviving cannibalism one unit of time, with 'cannibalism coefficients' c_{EL}/V, c_{EA}/V, $c_{PA}/V > 0$. Habitat size V has units equal to the volume occupied by 20 g of flour, the amount of medium routinely used in our laboratory.

The LPA model has explained and predicted successfully non-linear phenomena in a variety of contexts, including transitions between dynamic regimes (Dennis *et al.* 1995, 1997, 2001; Costantino *et al.* 1997), multiple attractors and resonance (Costantino *et al.* 1998; Henson *et al.* 2002), phase switching (Henson *et al.* 1998), saddle influences (Cushing *et al.* 1998), the use of small perturbations to control insect outbreaks (Desharnais *et al.* 2001), and lattice effects (Henson *et al.* 2001; King *et al.* 2002). Several aspects of this research are described in Cushing *et al.* (2003).

The two-species deterministic competition LPA model is a direct extension of the single species model:

$$l_{t+1} = ba_t \exp\left(-\frac{c_{el}}{V}l_t - \frac{c_{ea}}{V}a_t - \frac{c_{eL}}{V}L_t - \frac{c_{eA}}{V}A_t\right)$$

$$p_{t+1} = (1 - \mu_l)l_t$$

$$a_{t+1} = p_t \exp\left(-\frac{c_{pa}}{V}a_t - \frac{c_{pA}}{V}A_t\right) - (1 - \mu_a)a_t$$

$$L_{t+1} = BA_t \exp\left(-\frac{c_{El}}{V}l_t - \frac{c_{Ea}}{V}a_t - \frac{c_{EL}}{V}L_t - \frac{c_{EA}}{V}A_t\right)$$

$$P_{t+1} = (1 - \mu_L)L_t$$

$$A_{t+1} = P_t \exp\left(-\frac{c_{Pa}}{V}a_t - \frac{c_{PA}}{V}A_t\right) - (1 - \mu_A)A_t.$$

For notational convenience, 'species one' is represented by lower-case letters, while 'species two' is represented by upper-case letters. Each species has its own larval recruitment and death rates, and in addition to the intraspecific non-linearities there are non-linear interactions between the two species. Each species preys on the eggs and pupae of the other species, as well 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

PARAMETER VALUES

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 $V = 8/20 = 0{\cdot}4$. 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): $b = B = 10$, $\mu_l = \mu_L = 0{\cdot}2$, $\mu_a = \mu_A = 0{\cdot}02$, $c_{el} = c_{EL} = c_{El} = c_{eL} = 0{\cdot}01$, $c_{ea} = c_{EA} = c_{Ea} = c_{eA} = 0{\cdot}01$. 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 $c_{Pa} = 0{\cdot}005$, $c_{pA} = 0{\cdot}008$, $c_{pa} = 0{\cdot}01$ and $c_{PA} = 0{\cdot}012$.

MODEL OUTCOMES

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 outcome and was the hypothesis used by Leslie *et al.* (1968: 11) to explain the outcomes of their experiment.

In region E there is a stable, positive two-cycle with a large basin of attraction, which exists in the presence of two stable competitive exclusion equilibria. Certain initial conditions for which one species has a large advantage result in the extinction of the other; initial conditions with roughly equal numbers of each species result in two-cycle coexistence. This multiple attractor mix of initial state-dependent coexistence and competitive exclusion is a non-Lotka–Volterra scenario. This unexpected prediction of the competition LPA model is robust both in the sense that the set of initial conditions that lead to coexistence is large and that the dynamics in region E persist for arbitrarily large values of $c_{eL} = c_{El}$.

Although region D displays the familiar Lotka–Volterra dynamics described above, there is a fascinating non-linear dynamic phenomenon which occurs in this region. The presence of stable two-cycle coexistence attractor for slightly higher values of $c_{eL} = c_{El}$ (in region E) has the effect of causing long transient coexistence in region D before eventual extinction.

HYPOTHESIS TO EXPLAIN THE COEXISTENCE AND EXCLUSION DATA

The original interpretation of the Leslie experiment was based on the Leslie–Gower model. We are suggesting an alternative interpretation for these data based on the competition LPA model. Interestingly, in some circumstances the models have remarkably similar dynamic properties, while in other circumstances they can have significant differences. Our interpretation of the *Tribolium* data leans on both the similarities and the differences. First, we point out a similarity. The LPA model (in region D) and the Leslie–Gower model (as parameterized in Leslie *et al.* 1968) forecast the same long-term outcome for each of the 25 mixed species cultures: species exclusion. Moreover, both models are in agreement with each other and with the experimental observations (see Table 3 in Leslie *et al.* 1968) as to which species is excluded (see Fig. 3, Region D). Secondly, we point out a model difference. A property of the LPA model, which is not a feature of the Leslie–Gower

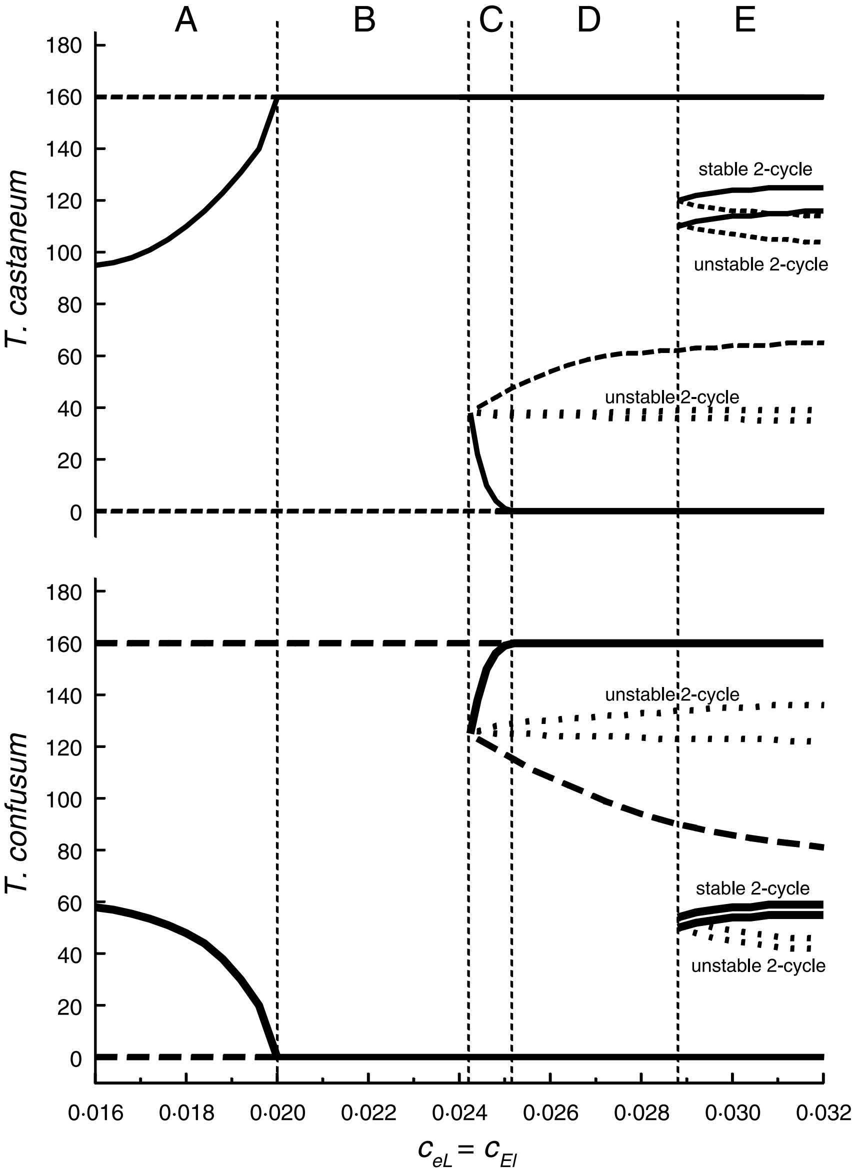

Fig. 2. The bifurcation diagram shows the dynamic behaviour of the two-species LPA model as c_{eL} and c_{El} change simultaneously from 0·016 to 0·032. The five regions are denoted by the letters A, B, C, D and E. The solid lines indicate stable equilibria and stable cycles. The broken lines identify unstable equilibria and unstable cycles. See text and Fig. 3 for further details.

formulation, is that an increase in interspecific interaction can result in a stable coexistence two-cycle. Beyond the grasp of the Leslie–Gower model but well within the context of the Leslie experiment we discover that coexistence in *Tribolium* is possible.

Our hypothesis for the explanation of the Leslie experiment and, in particular, the time–series data in the top panel of Fig. 1 is as follows. In the context of the competition LPA model, we interpret the Leslie experiment in terms of the dynamics forecast by region D of the bifurcation diagram given in Fig. 2. Leslie *et al.* state that change of some sort may have occurred in the 'coexistence' culture during the nearly 3-year experiment. In a discussion of the type of competitive system between *T. confusum* bI and *T. castaneum* cIV-a (Leslie *et al.* 1968: 11), we find the statement: 'It was quickly apparent from an analysis of the adult numbers at the time of the second census on day 60, that a change had occurred in the strain bI and that it now had, relatively speaking, a much greater "effect", presumably by way of cannibalistic powers, on cIV than it possessed originally.' Consistent with the latter statement (although far from definitive proof), we speculate that a small increase in interspecific competition occurred such that the 'coexistence' culture moved from region D into the neighbouring region E where there is model-predicted coexistence.

We now turn to the data. In Table 7 of Leslie *et al.* (1968), the adult census histories of three cultures are given: the 'coexistence' culture started with 4 cIV-a adults and 32 bI adults, a culture started with 8 cIV-a adults and 64 bI adults, and a culture started with 4 cIV-a adults and 64 bI adults. These data are presented on the left-hand side of Fig. 4. Even in the laboratory, noise is common to all ecological systems. Consequently, we used a stochastic version of the competition

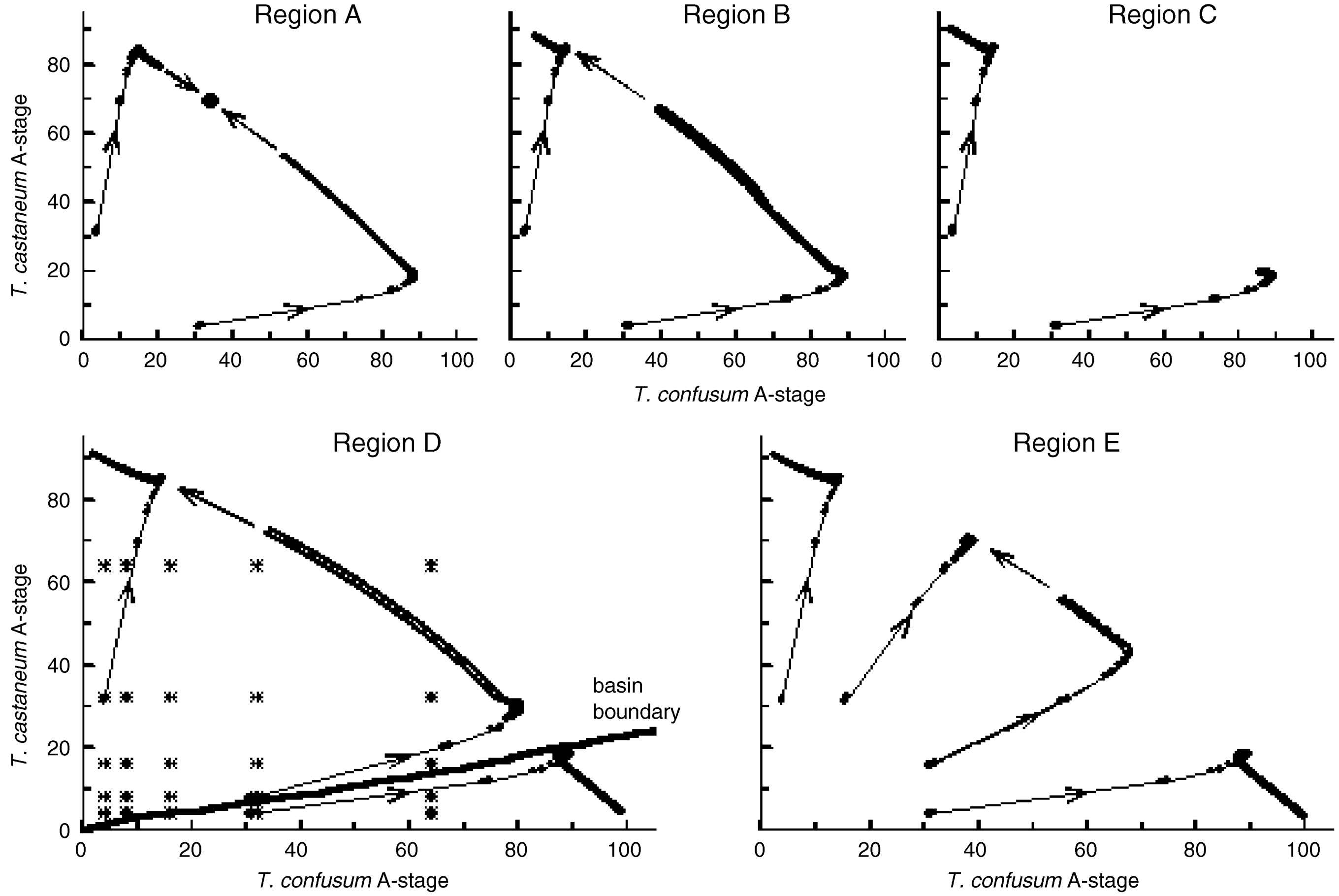

Fig. 3. Phase space graphs of representative deterministic LPA model orbits for the regions A, B, C, D and E given in Fig. 2. Region A, $c_{eL} = c_{El} = 0{\cdot}018$: classical Lotka–Volterra type dynamics with a globally attracting equilibrium; all positive initial conditions result in equilibrium coexistence. Region B, $c_{eL} = c_{El} = 0{\cdot}022$: 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, $c_{eL} = c_{El} = 0{\cdot}0244$: 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, $c_{eL} = c_{El} = 0{\cdot}028$: 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, $c_{eL} = c_{El} = 0{\cdot}032$: non-classical Lotka–Volterra dynamics. A saddle-node bifurcation of the composite map gives rise to a stable, positive two-cycle with a large basin of attraction, which exists in the presence of stable equilibria on both axes. We place the 'coexistence culture' (bI = 32, cIV-a = 4) in this region.

LPA model to obtain model predicted time–series. The stochastic version of the model adds random noise on a square root scale (Dennis *et al.* 2001; Cushing *et al.* 2003). On the right-hand side of Fig. 4 are representative stochastic model orbits corresponding to each of the observed adult census histories. In each case, there is a stunning degree of similarity between the data and the corresponding stochastic simulation. The introduction of stochastic population models was an important contribution to ecology by Park and colleagues (Simberloff 1980). Stochastic population models continue to enhance our understanding of ecological dynamics. Stochasticity incorporated as an integral component of the model provides explanations of patterns appearing in data that are not explained by either deterministic or stochastic forces alone (Bjornstad & Grenfell 2001; Benton *et al.* 2002; Cushing *et al.* 2003).

Discussion

The implications of the famous Lotka–Volterra competition model have played a large role in ecological theory and practice. The principle of competitive exclusion (Hardin 1960; Grover 1997) was formulated to a large extent from this and other mathematical models of competition that predict the coexistence of no more than one species on one limiting resource (Smith & Waltman 1995). Mathematicians, however, have known of theoretical exceptions to this principle for many years. The classical Lotka–Volterra type competition models incorporate several homogeneity assumptions that greatly limit the possible competitive outcomes. These include the assumptions that populations live in a homogeneous habitat under constant temporal conditions and consist of identical individuals. The limited number of Lotka–Volterra competition

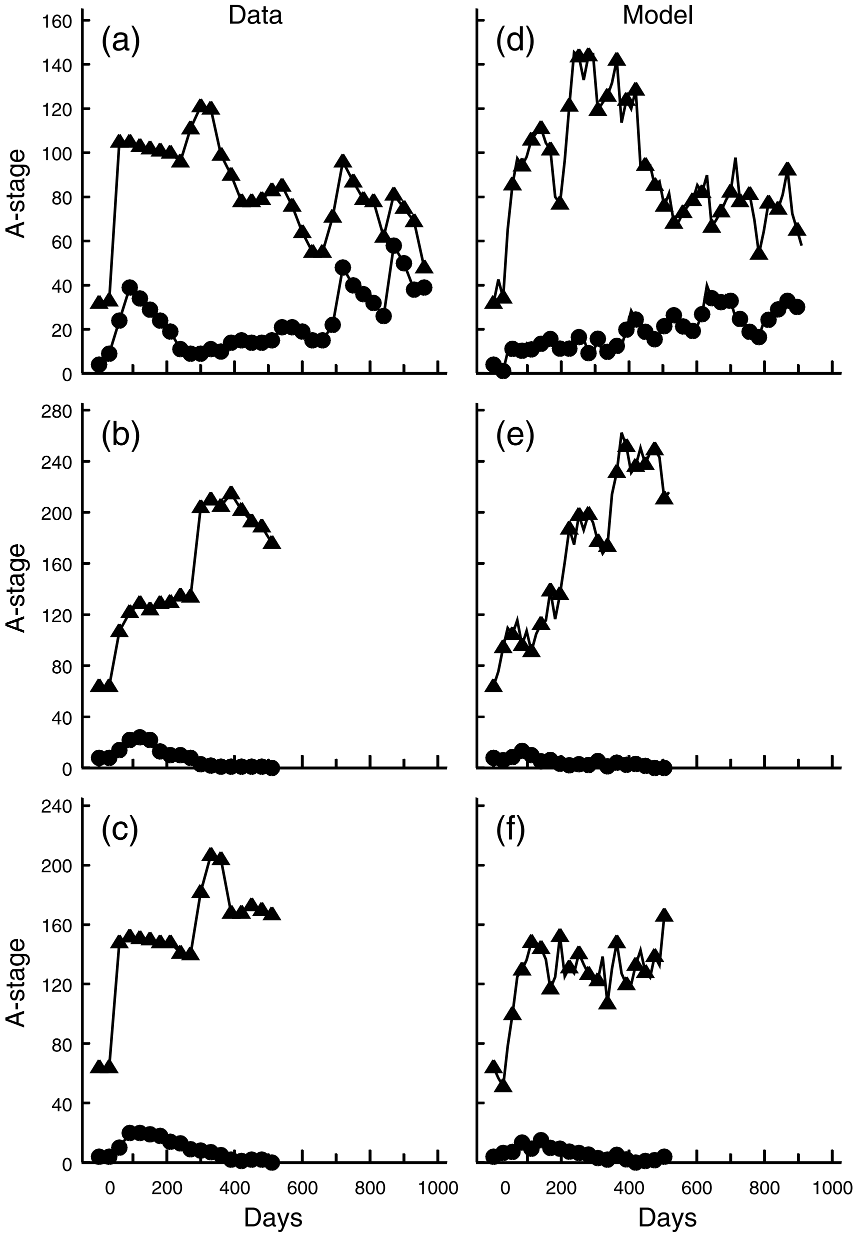

Fig. 4. Data and stochastic model simulations. Three observed adult time–series data are presented on the left hand side: (a) the 'coexistence' culture started with 4 cIV-a adults (circles) and 32 bI adults (triangles); (b) a culture started with 8 cIV-a adults and 64 bI adults in which cIV-a went extinct at day 510; and (c) a culture stated with 4 cIV-a adults and 64 bI adults in which cIV-a went extinct at day 510. On the right-hand side of the figure are representative stochastic model orbits with the same initial conditions as in the experimental cultures; (d) $c_{eL} = c_{El} = 0{\cdot}031$, region E in Fig. 2; (e) $c_{eL} = c_{El} = 0{\cdot}028$, region D in Fig. 2; (f) $c_{eL} = c_{El} = 0{\cdot}028$, region D in Fig. 2.

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 that they allow for non-equilibrium coexistence. As we have seen in this paper, the competition LPA model is an example that permits the coexistence of two species in periodically oscillating states. Moreover, in the circumstances investigated in this paper, the competition LPA model predicts oscillatory coexistence when interspecific competition is sufficiently strong. This is an unexpected result from the viewpoint of classical competition theory, which is founded on the opposite notion, namely that competitive exclusion occurs when interspecific competition is strong. Recently, in a consumer/resource model, Vandermeer *et al.* (2002) also show the counterintuitive result that increased competition can promote species coexistence. Their model involves an entirely different ecological scenario from that of the competition LPA model and entails increased competition by means of an increase in the number of competing species present in an ecological system.

It is intriguing that Park's competition experiments, although cited widely for over half a century as evidence of competitive exclusion, may include evidence of its failure. The competition LPA model provides an explanation for the 'difficult to interpret' *Tribolium* data reported by Leslie *et al.* (1968) that could not be obtained by these authors using Lotka–Volterra dynamics. The LPA model does this by allowing for the simultaneous occurrence of coexistence and exclusion attractors, specifically in this case, two competitive exclusion equilibria and a coexistence two-cycle. With a Lotka–Volterra mindset, Leslie *et al.* (1968) could not explain coexistence in the presence of two empirically observed exclusion equilibria.

The experimental data from Park's experiments cannot be tied to the competition LPA model with the rigour that this model has been tied to recent (single species) *Tribolium* experiments (Dennis *et al.* 1995; Dennis *et al.* 2001; Cushing *et al.* 2003). We do not have all of Park's data; moreover, he did not census larval and pupal stages and he did not census on the time scale of the LPA model. None the less, we can say that competitive coexistence is predicted by the LPA competition model for parameter values very near those estimated in recent experiments. We plan to design and implement experiments with two species of *Tribolium* in an effort to investigate the coexistence predicted by the LPA model in more detail. Should this contradiction to the classical principle of competitive exclusion be documented further by future experiments, a natural question arises regarding the nature of biological mechanisms and interactions that occur when two very similar species coexist in an oscillatory fashion. That is to say, is there some biological explanation for 'how' two such species manage coexistence in this way? One possible hint lies in the LPA model predictions themselves. The model predicted coexistence two-cycles do not oscillate out of phase (which, had they done so, might have suggested a kind of temporal sharing of their niche). Instead, the life-cycle stages oscillate in phase, which in effect decreases the interactions among the cannibalistic (adult and larval) stages and the egg and pupal stages. This reduces the 'amount' of interspecific competition on the victim stages. Counterintuitively, in order to establish the oscillations necessary for this synchronization of the life-cycle stages, the competitive 'intensity' of the interspecific cannibalism must be sufficiently strong (i.e. the per adult or larva cannibalism rates sufficiently high). It remains to be seen whether this particular mechanism will provide an explanation for coexistence in *Tribolium*, or whether some other explanation will surface. Nevertheless, we see from this example that the kinds of biological factors ignored by the Lotka–Volterra theory allow a rich variety of competitive scenarios and provide opportunities for species coexistence and ecological diversity.

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References

Benton, T.G., Lapsley, C.T. & Beckerman, A.P. (2002) The population response to environmental noise: population size, variance and correlation in an experimental system. *Journal of Animal Ecology*, **71**, 320–332.

Bjornstad, O.N. & Grenfell, B.T. (2001) Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, **293**, 638–643.

Chesson, P. (1985) Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology*, **28**, 263–287.

Cole, L.C. (1960) Competitive exclusion. *Science*, **132**, 348–349.

Costantino, R.F., Cushing, J.M., Dennis, B., Desharnais, R.A. & Henson, S.M. (1998) Resonant population cycles in temporally fluctuating habitats. *Bulletin of Mathematical Biology*, **60**, 247–273.

Costantino, R.F. & Desharnais, R.A. (1991) *Population Dynamics and the Tribolium Model: Genetics and Demography*. Springer-Verlag, New York.

Costantino, R.F., Desharnais, R.A., Cushing, J.M. & Dennis, B. (1997) Chaotic dynamics in an insect population. *Science*, **275**, 389–391.

Crowe, K.M. (1991) *A discrete size-structured competition model*. PhD Dissertation, Interdisciplinary Program in Applied Mathematics, University of Arizona, Tucson.

Cushing, J.M. (1980) Two species competition in a periodic environment. *Journal of Mathematical Biology*, **10**, 385–400.

Cushing, J.M. (1983) *Periodic Lotka–Volterra Systems and Time Sharing of Ecological Niches*. Lecture Notes in Biomathematics, 52, pp. 342–348. Springer, Berlin.

Cushing, J.M. (1986) Periodic Lotka–Volterra competition equations. *Journal of Mathematical Biology*, **24**, 381–403.

Cushing, J.M. (1998) *An Introduction to Structured Population Dynamics*. CBMS-NSF Regional Conference Series on Applied Mathematics, 71. SIAM, Philadelphia.

Cushing, J.M., Costantino, R.F., Dennis, B., Desharnais, R.A. & Henson, S.M. (2003) *Chaos in Ecology: Experimental Nonlinear Dynamics*. Academic Press, London.

Cushing, J.M., Dennis, B., Desharnais, R.A. & Costantino, R.F. (1998) Moving toward an unstable equilibrium: saddle nodes in population systems. *Journal of Animal Ecology*, **67**, 298–306.

Cushing, J.M. & Saleem, M. (1984) *A Competition Model with Age-Structure*. Lecture Notes in Biomathematics, 54, pp. 178–192. pringer, Berlin.

Darwin, C. (1859) *The Origin of Species*. Mentor Book, New York [reprinted 1958].

Dennis, B., Desharnais, R.A., Cushing, J.M. & Costantino, R.F. (1995) Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. *Ecological Monographs*, **65**, 261–281.

Dennis, B., Desharnais, R.A., Cushing, J.M. & Costantino, R.F. (1997) Transitions in population dynamics: equilibria to periodic cycles to aperiodic cycles. *Journal of Animal Ecology*, **66**, 704–729.

Dennis, B., Desharnais, R.A., Cushing, J.M., Henson, S.M. & Costantino, R.F. (2001) Estimating chaos and complex dynamics in an insect population. *Ecological Monographs*, **71**, 277–303.

Desharnais, R.A., Costantino, R.F., Cushing, J.M., Henson, S.M. & Dennis, B. (2001) Chaos and population control of insect outbreaks. *Ecology Letters*, **4**, 229–235.

Edmunds, J. (2001) *A study of a stage-structured model of two competing species*. PhD Dissertation, University of Arizona, Tucson.

Freedman, H.I., So, J.H. & Waltman, P. (1989) Coexistence in a model of competition in the chemostat incorporating discrete delays. *SIAM Journal of Mathematical Analysis*, **49**, 859–870.

Gause, G.F. (1934) *The Struggle for Existence*. Hafner Press, New York [reprinted 1964].

Grover, J.P. (1997) *Resource Competition*. Population and Community Biology Series 19. Chapman & Hall, New York, 1997.

Hardin, G. (1960) The competitive exclusion principle. *Science*, **131**, 1292–1297.

Henson, S.M., Costantino, R.F., Cushing, J.M., Desharnais, R.A., Dennis, B. & King, A.A. (2001) Lattice effects observed in chaotic dynamics of experimental populations. *Science*, **294**, 602–605.

Henson, S.M., Costantino, R.F., Desharnais, R.A., Cushing, J.M. & Dennis, B. (2002) Basins of attraction: population dynamics with two stable 4-cycles. *Oikos*, **98**, 17–24.

Henson, S.M., Cushing, J.M., Costantino, R.F., Dennis, B. & Desharnais, R.A. (1998) Phase switching in population cycles. *Proceedings of the Royal Society London B*, **265**, 2229–2234.

Huisman, J. & Weissing, F.J. (1999) Biodiversity of plankton by species oscillations and chaos, *Nature*, **402**, 407–410.

Huisman, J. & Weissing, F.J. (2001) Fundamental unpredictability in multispecies competition. *American Naturalist*, **157**, 488–494.

King, A.A., Desharnais, R.A., Henson, S.M., Costantino, R.F., Cushing, J.M. & Dennis, B. (2002) Random perturbations and lattice effects in chaotic population dynamics. *Science*, **297**, 2163a.

Koch, A.L. (1974) Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. *Journal of Theoretical Biology*, **44**, 378–386.

Leslie, P.H. & Gower, J.C. (1958) The properties of a stochastic model for two competing species. *Biometrika*, **45**, 316–330.

Leslie, P.H., Park, T. & Mertz, D.B. (1968) The effect of varying the initial numbers on the outcome of competition between two *Tribolium* species. *Journal of Animal Ecology*, **37**, 9–23.

Levins, R. (1979) Coexistence in a variable environment. *American Naturalist*, **114**, 765–783.

Li, B. (2001) Periodic coexistence in the chemostat with three species competing for three essential resources. *Mathematical Biosciences*, **174**, 27–40.

Loreau, M. & Ebenhoh, W. (1994) Competitive exclusion and coexistence of species with complex life cycles. *Theoretical Population Biology*, **46**, 58–77.

May, R.M. (1974) *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.

McGehee, R. & Armstrong, R. (1977) Some mathematical problems concerning the ecological principle of competitive exclusion. *Journal of Difference Equations*, **23**, 30–52.

de Mottoni, P. & Schiaffino, A. (1981) Competition systems with periodic coefficients: a geometric approach. *Journal of Mathematical Biology*, **11**, 319–355.

Namba, T. (1984) Competitive co-existence in a seasonally fluctuating environment. *Journal of Theoretical Biology*, **111**, 369–386.

Namba, T. (1986) Bifurcation phenomena appearing in the Lotka–Volterra competition equations: a numerical study. *Mathematical Biosciences*, **81**, 191–212.

Namba, T. & Takahashi, S. (1993) Competitive coexistence in a seasonally fluctuating environment. II. Multiple stable states and invasion success. *Theoretical Population Biology*, **44**, 374–402.

Park, T. (1948) Experimental studies of interspecies competition. I. Competition between populations of the flour beetles *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecological Monographs*, **18**, 265–308.

Park, T. (1954) Experimental studies of interspecies competition. II. Temperature, humidity and competition in two species of *Tribolium*. *Physiological Zoology*, **27**, 177–238.

Park, T. (1957) Experimental studies of interspecies competition. III. Relation of initial species proportion to the competitive outcome in populations of *Tribolium*. *Physiological Zoology*, **30**, 22–40.

Park, T., Leslie, P.H. & Mertz, D.B. (1964) Genetic strains and competition in populations of *Tribolium*. *Physiological Zoology*, **37**, 97–162.

Park, T., Nathanson, M., Ziegler, J.R. & Mertz, D.B. (1970) Cannibalism of pupae by mixed-species populations of adult *Tribolium*. *Physiological Zoology*, **43**, 166–184.

Simberloff, D. (1980) A succession of paradigms in ecology: Essentialism to materialism and probabilism. *Synthese*, **43**, 3–39.

Smith, H.L. & Waltman, P. (1995) *The Theory of the Chemostat: Dynamics of Microbial Competition*. Cambridge Studies in Mathematical Biology 13. Cambridge University Press, Cambridge.

Vandermeer, J.M.A., Evans, P., Foster, T., Ho, M., Reiskind & Wund M. (2002) Increased competition may promote species coexistence. *Proceedings of the National Academy of Sciences USA*, **99**, 8731–8736.

Waltman, P. (1983) *Competition Models in Population Biology*. CBMS-NSF regional Conference Series in Applied Mathematics, 45. SIAM, Philadelphia.

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