Bifurcations and chaos in a predator–prey system with the Allee effect

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It is known from many theoretical studies that ecological chaos may have numerous significant impacts on the population and community dynamics. Therefore, identification of the factors potentially enhancing or suppressing chaos is a challenging problem. In this paper, we show that chaos can be enhanced by the Allee effect. More specifically, we show by means of computer simulations that in a time-continuous predator–prey system with the Allee effect the temporal population oscillations can become chaotic even when the spatial distribution of the species remains regular. By contrast, in a similar system without the Allee effect, regular species distribution corresponds to periodic/quasi-periodic oscillations. We investigate the routes to chaos and show that in the spatially regular predator–prey system with the Allee effect, chaos appears as a result of series of period-doubling bifurcations. We also show that this system exhibits period-locking behaviour: a small variation of parameters can lead to alternating regular and chaotic dynamics.

Keywords: Allee effect; predator–prey system; patchiness; chaos; period locking

1. INTRODUCTION

The manifestation of chaos in ecosystems dynamics has been an issue of intense discussion during the past three decades (May 1976; Scheffer 1991; Hastings *et al.* 1993; Rinaldi & De Feo 1999; Cushing *et al.* 2003). Many theoretical studies have demonstrated that ecological chaos, if and when it exists, can affect many important ecosystem features such as predictability (Scheffer 1991), species persistence (Allen *et al.* 1993; Jansen 1995) and biodiversity (Huisman & Weissing 1999). Another reason that makes this subject so controversial is that, in spite of a growing number of indications (Ellner & Turchin 1995; Perry *et al.* 2000), conclusive evidence of chaos in ecological data has never been shown, although there does exist solid evidence of chaos in a real population under laboratory conditions (Costantino *et al.* 1997). One problem is often seen in an insufficient length of available ecological time series; moreover, it is currently not clear whether suitable time series can be obtained at all because of the impact of long-term environmental fluctuations (Dennis *et al.* 2001; Hastings 2001). Another serious problem is immaturity of the theoretical approaches used to argue chaos from field data, especially under the impact of noise (Dennis *et al.* 2003). In this situation, a better understanding of mechanisms responsible for transitions between different types of dynamics and the identification of factors that can potentially enhance or suppress chaotic dynamics are becoming the issues of primary importance. One way to study these issues is through controlled laboratory experiments (cf. Costantino *et al.* 1997; Cushing *et al.* 2003); a useful insight into the problem can also be made by means of mathematical modelling and computer simulations.

While early theoretical studies of ecological chaos were concerned with the temporal dynamics of spatially homogeneous systems, the progress made during the past decade has been to a large extent stipulated by the understanding of the role of space (De Roos *et al.* 1991; Rand & Wilson 1995; Sole & Bascompte 1995). In particular, it was shown that the system's capability to manifest chaotic dynamics is essentially different in the spatially homogeneous and inhomogeneous cases. The reason is that, in an autonomous time-continuous system, chaos is possible only when the dimension of the corresponding state space is greater than 2. In population dynamics this fact is often interpreted in terms of the number of interacting populations: assuming that each population can be described by a single scalar variable (and there is no other dynamical variable in the system), chaos appears possible in a community of three or more species (Gilpin 1978; Hastings & Powell 1991; Rinaldi & De Feo 1999). (Note that time-discrete models can exhibit chaotic dynamics even in the single-species case; see May 1976.) However, when the condition of spatial homogeneity is relaxed, cf. 'models with explicit space', chaos was observed already in a two-species predator–prey system both in a space-discrete metapopulation model (Jansen 1995) and in a space-continuous model (Pascual 1993; Sherratt *et al.* 1995; Pascual & Caswell 1997; Petrovskii & Malchow 1999, 2001). In the latter case, transition to chaos was attributed to the formation of irregular spatial patterns. The patterns are self-organized in the sense that they are not induced by environmental inhomogeneity or specific initial conditions. As a result of the pattern formation, the domain appears to be dynamically split into a number of virtually independent subdomains so that the population dynamics inside each of them is practically unaffected by the dynamics inside the others (Petrovskii & Malchow 2001; Petrovskii *et al.* 2003). From a dynamical systems perspective, chaos in that system becomes possible because splitting into several spatial subdomains increases

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the number of the state variables. Remarkably, if the populations' distribution over space is regular, the system exhibits periodic or quasi-periodic dynamics (Petrovskii & Malchow 1999, 2001; Sherratt 2001).

The question naturally arising here is whether that prominent spatial irregularity in the population distribution is a necessary property of chaos in a few-species ($N \leq 2$) system. The above results were obtained for the space- and time-continuous predator-prey system where the prey population exhibits logistic growth. However, in real ecosystems species growth is often damped by the Allee effect (Allee 1938). The Allee effect was shown to strongly affect not only local population dynamics (Dennis 1989) but also population interactions in space (Lewis & Kareiva 1993; Amarasekare 1998; Gyllenberg *et al.* 1999; Petrovskii *et al.* 2002a,b). However, the impact of the Allee effect on the properties of chaos in a population system has never been studied in detail.

In this paper, we consider the properties of chaos in a predator-prey system with the Allee effect for the prey. We show by means of computer simulations that in this system temporal chaotic fluctuations of population size and population density can occur even when the species distribution over space remains remarkably regular, having the form of two standing symmetric patches. We then consider scenarios of transition to chaos in this system by varying some of the parameters and show that chaos appears through the succession of period-doubling bifurcations. Also, we show that the system exhibits period-locking behaviour (cf. Cushing *et al.* 2003) so that parameter domains corresponding to chaos alternate with the domains corresponding to regular dynamics.

2. MAIN EQUATIONS

We consider the following model of predator-prey interaction in a homogeneous environment:

$$\frac{\partial H(X,T)}{\partial T} = D_1 \frac{\partial^2 H}{\partial X^2} + F(H) - f(H,P), \quad (2.1)$$

$$\frac{\partial P(X,T)}{\partial T} = D_2 \frac{\partial^2 P}{\partial X^2} + \kappa f(H,P) - MP \quad (2.2)$$

(cf. Segel & Jackson 1972; Nisbet & Gurney 1982; Murray 1989; Holmes *et al.* 1994; Sherratt 2001). Here, H and P are the densities of prey and predator, respectively, at moment T and position X . D_1 and D_2 are diffusivities and κ is the food utilization coefficient. The function $F(H)$ describes prey multiplication, $f(H,P)$ describes predation, and the term MP stands for predator mortality. To keep the model as simple as possible (see also the end of § 4), we assume that $f(H,P) = AHP$, where A is the predation rate, which corresponds to the classical Volterra scheme.

Assuming Allee dynamics for the prey population, its growth rate can be parameterized as follows (Lewis & Kareiva 1993):

$$F(H) = \frac{4\omega}{(K - H_0)^2} H(H - H_0)(K - H), \quad (2.3)$$

where K is the prey-carrying capacity, ω is the maximum *per capita* growth rate and H_0 quantifies the intensity of the Allee effect so that it is called 'strong' if $0 < H_0 < K$

(when the growth rate becomes negative for $H < H_0$) and 'weak' if $-K < H_0 \leq 0$ (Owen & Lewis 2001; Wang & Kot 2001). For $H_0 \leq -K$, the Allee effect is absent (Lewis & Kareiva 1993).

Equations (2.1)–(2.3) contain a large number of parameters, which makes their numerical investigation cumbersome. However, by choosing appropriate scales for the variables (Nisbet & Gurney 1982; Murray 1989; for a more general discussion see Barenblatt 1996), the number of parameters can be lessened. Considering dimensionless variables $u = H/K$, $v = P/(\kappa K)$, $t = aT$, $x = X(a/D_1)^{1/2}$, where $a = A\kappa K$, from equations (2.1) and (2.2), we obtain

$$\frac{\partial u(x,t)}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \gamma u(u - \beta)(1 - u) - uv, \quad (2.4)$$

$$\frac{\partial v(x,t)}{\partial t} = \varepsilon \frac{\partial^2 v}{\partial x^2} + uv - \delta v. \quad (2.5)$$

Equations (2.4) and (2.5) contain four dimensionless parameters (against eight in the original equations), i.e. $\beta = H_0/K$, $\gamma = 4\omega K/(A\kappa(K - H_0)^2)$, $\delta = M/a$ and $\varepsilon = D_2/D_1$. Thus, the behaviour of dimensionless solutions u and v appears to depend on four dimensionless combinations of the original parameters rather than on each of them separately.

System (2.4) and (2.5) has recently been considered by Morozov (2003) and Petrovskii *et al.* (2002a,b, 2004) in connection with biological invasion. The species spread was studied for the following initial conditions:

$$u(x,0) = u_0 \text{ for } -\frac{1}{2}\Delta_u < x < \frac{1}{2}\Delta_u, \text{ otherwise } u(x,0) = 0, \quad (2.6)$$

$$v(x,0) = v_0 \text{ for } -\frac{1}{2}\Delta_v < x < \frac{1}{2}\Delta_v, \text{ otherwise } v(x,0) = 0, \quad (2.7)$$

where u_0 , v_0 are the initial population densities and Δ_u , Δ_v give the size of initially invaded domain. It was shown that, depending on the parameter values, in equations (2.4) and (2.5) describes a wide variety of the regimes of species invasion. Some of them appear to be qualitatively similar to those observed earlier in the predator-prey system without the Allee effect, e.g. the propagation of population fronts with excitation of chaotic spatio-temporal oscillations in the wake of invasion (cf. Sherratt *et al.* 1995). However, a few new regimes of the system dynamics that were essentially attributed to the impact of the Allee effect have also been observed (Petrovskii *et al.* 2002a,b; Morozov 2003). One of them, the regime of formation of spatially regular standing (quasi)stationary patches will be considered in § 3 as a paradigm of transition to chaos not linked to spatial irregularity.

3. RESULTS OF COMPUTER SIMULATIONS

System (2.4)–(2.5) with the initial conditions (2.6) and (2.7) was solved numerically in the domain $-\frac{1}{2}L < x < \frac{1}{2}L$ by the finite-difference method using the implicit scheme. The steps of the numerical mesh were chosen as $\Delta x = 0.2$ and $\Delta t = 0.001$ and it was checked that a further decrease of the step values did not lead to any significant modification of the results. The 'no-flux' condition was used at the boundaries and the length L of the numerical

Figure 1. Population density versus space (solid curve for prey, dashed curve for predator) calculated from equations (2.4) and (2.5) at different times for parameters $\beta = 0.34$, $\delta = 0.6$, $\gamma = 5$, $\varepsilon = 1$, $L = 100$ and initial distribution (2.6)–(2.7) with $u_0 = 1$, $v_0 = 0.1$, $\Delta_u = 19$, $\Delta_v = 4$. Note that except for the early stage ($t \leq 100$) the position of the patch centres does not change in the course of system dynamics. (a) $t = 240$, (b) $t = 710$ and (c) $t = 1200$.

domain was chosen large enough to make the impact of the boundaries as small as possible during the simulation time.

We want to mention that, owing to the Allee effect, the dynamics of system (2.4)–(2.5) depends on the initial conditions (cf. Lewis & Kareiva 1993): if u_0 and/or Δ_u are small (e.g. $u_0 < \beta$) or v_0 is large, the species go extinct (the impact of Δ_v is less prominent). As consideration of this threshold phenomenon is beyond the scope of this paper, in the computer simulations parameters u_0 , Δ_u and v_0 have always been chosen sufficiently large and sufficiently small, respectively.

Figure 1 gives an example of standing quasi-stationary patches showing the population densities calculated at $t = 240$ (a), $t = 710$ (b) and $t = 1200$ (c) for $\beta = 0.34$, $\delta = 0.6$, $\gamma = 5$, $\varepsilon = 1$, $u_0 = 1$, $v_0 = 0.1$, $\Delta_u = 19$, $\Delta_v = 4$ and

$L = 100$. For this regime, an early evolution of the initial species distribution leads to the formation at $t \approx 100$ of two dome-shaped patches, see figure 1a. During the later stages of the system dynamics, the position of the patch centres remains constant while the population densities in the patches profile oscillate with time, as in figure 1a–c. Similar behaviour can be observed for somewhat different parameter values, e.g. in the case where β and γ are fixed as above, for δ between 0.597 and 0.637. For the values of δ close to the right-hand end of this interval, the oscillations in the patches profile cease and the population distribution over space becomes stationary.

As the population density is of an apparently different order of magnitude near the patch centres and between them (e.g. for $x \approx 0$), to quantify the dynamics of the system as a whole we consider the population size of prey and predator:

$$U(t) = \int_{-L/2}^{L/2} u(x, t) dx, \quad V(t) = \int_{-L/2}^{L/2} v(x, t) dx. \quad (3.1)$$

Our main goal is to acquire an insight into the properties of the population oscillations in the patch profile and how these properties may change with a change in the parameter values. For that purpose, we fix the values of β , γ and ε as above and perform a large number of computer simulations corresponding to different δ (the effect of other parameters' variation will be considered in § 4). For each δ , system (2.4)–(2.5) with the initial conditions (2.6)–(2.7) is solved over sufficiently large time (to allow the transients to die out) and the properties of the system dynamics at large time are analysed in terms of population sizes U and V .

We start with $\delta = 0.637$ and consider how the system dynamics changes with a decrease in δ . For δ only slightly less than this value, the population densities relax, in the course of time, to a stationary dome-shaped distribution (similar to that shown in figure 1a), which corresponds to a point in the (U, V) -phase plane. We obtain the result that stationarity breaks at $\delta = 0.6185$ and for $0.6036 \leq \delta \leq 0.6185$ the system exhibits periodic oscillations; see figure 2a(i), b(i). At $\delta = 0.6036$, a period-doubling bifurcation takes place; cf. figure 2a(ii), b(ii). More period-doubling bifurcations take place for smaller values of δ and, as a result of this cascade, the dynamics of the system becomes chaotic at $\delta = 0.6009$; see figure 2a(iii), b(iii).

To prove more rigorously that what is shown in figure 2a(iii), b(iii) is really chaos, we estimate the dominant Lyapunov exponent λ . For that purpose, we induce a small perturbation to the patches and then consider the behaviour of the following value:

$$\Delta M(t) = \{[U_2(t) - U_1(t)]^2 + [V_2(t) - V_1(t)]^2\}^{1/2}, \quad (3.2)$$

where U_1 and V_1 and U_2 and V_2 are the values of the prey and predator population sizes in the undisturbed and disturbed system, respectively. Thus, ΔM gives the distance between the two initially close systems' trajectories. The perturbation is applied at time $t_0 = 1200$ to exclude possible impact of the transients, and $\Delta M(t_0)$ is varied between 10^{-7} and 10^{-12} .

Figure 2. A cascade of period-doubling bifurcations leading to the onset of chaotic oscillations: (a) trajectory of the system dynamics in the phase plane (U, V) for different values of predator mortality, (i) $\delta = 0.607$, (ii) $\delta = 0.602$ and (iii) $\delta = 0.6$. Other parameters are the same as in figure 1. (b) The corresponding power spectra of the prey population size. Note that, in spite of chaos, the spatial population distribution remains regular; cf. figure 1.

To test the procedure, we first apply it to the case of periodic dynamics. We obtain the result that $\Delta M(t)$ never exceeds 10^{-7} and the estimated value of λ is zero (within the computation error) as is predicted by theory. We then apply the procedure to the case shown in figure 2a(iii), b(iii). For this regime, we obtain the result that there is an exponential discrepancy between the close trajectories, i.e. $\Delta M(t) \approx \exp[\lambda(t - t_0)]$ where λ is positive and its value is estimated as $\lambda = 0.009 \pm 0.001$. Note that, in spite of chaotic temporal oscillations of the population size, the spatial distribution of the populations remains fairly regular; see figure 1 obtained for exactly the same parameter values as in figure 2a(iii), b(iii).

It appears, however, that a further decrease in δ restores regularity in temporal oscillations. Figure 3a shows the (U, V)-phase plane obtained for $\delta = 0.5998$. The dynamics is periodic in this case, although the form of the cycle is

rather complicated. A further decrease in δ leads to another period-doubling cascade (cf. figure 3a(i,ii), b(i,ii)) and for $\delta = 0.5993$ the dynamics becomes chaotic again with the dominant Lyapunov exponent estimated as $\lambda = 0.016 \pm 0.001$. We stress that in this case, again, the population distribution over space is regular and qualitatively the same as shown in figure 1.

The above results are summarized in the form of the bifurcation tree shown in figure 4. To obtain the bifurcation tree, we apply the following procedure. For each value of δ , we first calculate the mean value of the predator population size V^* at the time interval $1000 < t < 4200$ (a smaller time has not been taken into account to make sure that the transients die out completely). The cross-section points between the horizontal straight line $V = V^*$ and the trajectory of the system dynamics in the (U, V)-phase plane during that time interval give the set of values

Figure 3. The next cascade of period-doubling bifurcations after regularity was restored: (a) trajectory of the system dynamics for (i) $\delta = 0.5998$, (ii) $\delta = 0.5996$ and (iii) $\delta = 0.5993$. Other parameters are the same as in figures 1 and 2. (b) The corresponding power spectra of the prey population size. In all cases the spatial distribution of the populations remains regular, having the form of two symmetric dome-shaped patches.

U_k , which are then plotted in figure 4. Apparently, in the case of stationary patches there is only one point corresponding to given δ (see the right-hand side of figure 4), in the case of simple periodic dynamics before the first period-doubling bifurcation there are only two points, and in the case of chaos the points form a 'dense' set spread over a certain interval corresponding to the size of the strange attractor; cf. figures 2a(iii), b(iii) and 3a(iii), b(iii).

The simulations fulfilled for δ from $0.597 \leq \delta \leq 0.5993$ show that chaos and regularity may also alternate in that parameter range; however, the intervals between the values of δ corresponding to chaos and regularity become so small there that it makes detailed investigation very difficult. For $\delta < 0.597$ the regime of standing patches gives way to the regime of species extinction (Petrovskii *et al.*

2002b; Morozov 2003) and for $\delta > 0.637$ it turns to the regime of patchy spread (Petrovskii *et al.* 2002a,b).

It should be noted that, as long as the values of u_0 , v_0 , Δ_u , Δ_v corresponding to species extinction are excluded (see the comment at the beginning of § 3), the results presented above appear to be robust to the choice of initial conditions. The initial conditions affect only the early stage of the system dynamics but not the later stage when the transients die out. Although minor details of the spatial pattern (e.g. the position of the patches) do depend on the initial species distribution, the regularity of the pattern is not affected by reasonably small variations of the initial conditions. The system dynamics exhibit essentially the same properties; in particular, the shapes of the attractors in figures 2 and 3 and the bifurcation tree in figure 4

Figure 4. The bifurcation diagram of the system (2.4)–(2.5) showing the changes in the system dynamics appearing from a decrease in the predator mortality rate δ . Other parameters are the same as in figures 1–3.

do not depend on the parameters of initial conditions (2.6) and (2.7).

4. CONCLUSIONS AND DISCUSSION

The Allee effect has been attracting much attention recently owing to its strong potential impact on population dynamics (Amarasekare 1998; Gyllenberg *et al.* 1999; Owen & Lewis 2001; Wang & Kot 2001; Petrovskii *et al.* 2002*a,b*). In this paper, we show that the Allee effect significantly increases the system's spatio-temporal complexity and may enhance chaos in population dynamics; in the predator–prey system with the Allee effect, chaotic temporal population oscillations can appear in the case when the spatial distribution of the species remains regular. By contrast, a spatially regular species distribution in the system without the Allee effect can only lead to periodic/quasi-periodic population oscillations (Petrovskii & Malchow 1999, 2001; Sherratt 2001).

To visualize the system's dynamics, we used the values of population size U and V ; see equation (3.1). However, based on the results of our computer simulations we want to mention that the type of the oscillations in population size, i.e. periodic or chaotic, conforms to the type of the (local) oscillations in population density. Particularly, chaos in the dynamics of population size always corresponds to local chaotic oscillations, although the magnitude of the oscillations is very different near the centre of the patches and between them.

A question of interest is whether our results are robust to parameter variations. To address this issue, we performed extensive computer simulations for different parameter values (in total, more than 100 parameter sets were examined). The results are summarized in figure 5, which shows a map in the (β, δ) parameter plane obtained for $\gamma = 5$ and $\varepsilon = 1$. It appears that the parameter range where species introduction leads to the formation of standing stationary/quasi-stationary patches (cf. figure 1) has the form of a stripe. Inside this domain there is a narrower stripe where chaos and period locking in temporal population oscillations are observed for a spatially regular population distribution. The parameters from above the

Figure 5. The map in the (β, δ) parameter plane showing the domain corresponding to the regime of standing stationary/quasi-stationary patches and the subdomain corresponding to chaos and period locking.

hatched domain correspond to species extinction, whereas the parameters from below the hatched domain correspond to species invasion. Depending on parameters, the invasion can take place either through propagation of a travelling population wave or through spreading of separate self-multiplying patches (cf. Petrovskii *et al.* 2002*a,b*; Morozov 2003). On the whole, the spatially extended predator–prey system with the Allee effect exhibits very rich dynamics, which will be described in detail elsewhere (Petrovskii *et al.* 2004).

Regarding the impact of other parameters, we have observed that variation of parameter γ does not make a significant impact, and chaos can be easily observed for values of γ from a wide range. We also emphasize that the regime of standing quasi-stationary patches along with chaotic oscillations in population size can also be observed if the diffusivity is different for prey and predator. For

$\varepsilon \neq 1$, the position of the chaotic domain in the (β, δ) plane changes slightly while its size decreases with an increase of the difference between ε and 1 so that for $\varepsilon < 0.5$ and $\varepsilon > 1.4$ chaotic oscillations become very difficult to observe. Note that this condition is not too restrictive if applied to real ecological communities. One example where the diffusivities of prey and predator are virtually equal is given by the plankton system, where spatial mixing mainly occurs owing to the impact of turbulence (Okubo 1980). (Remarkably, plankton systems have often been used as a paradigm of chaotic spatio-temporal dynamics; see Pascual 1993; Sherratt 2001; Medvinsky *et al.* 2002.) In addition, in terrestrial communities, although the individual motion of a predator tends to be faster than that of its prey, in many cases they are on the same order; examples may be given by lynx-hare and wolf-deer trophic pairs.

Analysis of the (β, δ) -plane structure thus leads to a clear understanding that the phenomenon as a whole (i.e. temporal chaos along with spatial regularity) should be essentially attributed to the impact of the strong Allee effect because the lower corner of the chaotic domain is always situated at a positive β ; see figure 5. For a weak Allee effect ($-1 < \beta \leq 0$) or when the Allee effect is absent ($\beta \leq -1$), chaotic oscillations of this type are not observed.

The existence of self-organized irregular spatial patterns has long been considered a 'fingerprint' of chaos (Comins *et al.* 1992; Nowak & May 1992) and was often linked to chaotic temporal fluctuations (Pascual 1993; Sherratt *et al.* 1995). However, the question remained open to what extent a spatial structure is necessary to enhance chaotic oscillations. In this paper, we show that the impact of the Allee effect can reduce the degree of required spatial heterogeneity and invokes temporal chaotic oscillations in a system where they would otherwise be impossible. Our results make a certain contribution towards a better understanding of possible levels of spatio-temporal complexity in ecological communities.

It should be noted that, if considered in a somewhat broader ecological perspective, our results have an intuitively clear meaning. There has been a growing understanding during the past years that, regarding the dynamics of real ecosystems, it is perhaps not chaos itself that is important but the transitions between different dynamical regimes arising as a result of perturbation of the system's parameters (cf. Cushing *et al.* 2003). From this standpoint, it seems interesting to know how the dynamics varies when the parameters move across the diagram shown in figure 5. For simplicity, let us assume that only one parameter is changing, either δ or β , others remaining fixed. A decrease in the predator mortality δ changes the regime of species invasion to the regime of standing patches and then to species extinction. Apparently, from a given species' perspective, invasion is a positive factor enhancing its regional persistence. A decrease in predator mortality destabilizes the system, hampers and eventually blocks species invasion, and thus potentially decreases species persistence. Similar effects are produced by an increase in β . These inferences appear to be in good agreement with current understanding of the impact of predation and the Allee effect on population dynamics.

In conclusion, we mention that the results of this paper were obtained under the assumption that predation is

described by the bilinear function of the prey and predator densities (see the lines below equations (2.1) and (2.2)). This assumption, however, is not crucial and has been made mainly to avoid additional parameters. Our computer experiments indicate that the system exhibits qualitatively similar behaviour when predator response is of Holling type II, e.g. $f(H, P) = AHP/(H + B)$, where B is another parameter, and the regime of standing quasi-stationary patches with chaotic oscillations can also be observed in this case.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.