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Limit cycles of a predator-prey model with intratrophic predation.

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Abstract

We present some properties of a differential system that can be used to model intratrophic predation in simple predator-prey models. In particular, for the model we determine the maximum number of limit cycles that can exist around the only fine focus in the first quadrant and show that this critical point cannot be a centre.

Key words: nonlinear differential equations, limit cycles

1 Introduction

In this paper we show how a planar dynamical system that is of mathematical interest to us can be used to model certain ecological relationships involving *intratrophic predation*. In modelling the dynamics of biological populations in ecosystems that involve large numbers of species it is seldom feasible to consider individual species [1]. Often aggregates of species are considered leading to simplified, but tractable, models. The simplest predator-prey systems involve two variables, representing the predator and the prey, and give rise to planar dynamical systems

$$\dot{x} = P(x, y), \quad \dot{y} = Q(x, y). \tag{1}$$

The dependent variables could be biomass or just the size of the populations and for convenience we always refer to the independent variable as time. The

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models describe the interaction of two *trophic levels* - for instance plants eaten by animals or one group of animals eaten by another higher up the food chain.

There may be intratrophic predation within one of the populations - members of one trophic group consuming members of the same group or even cannibalism within a species. Cushing [2] investigated the role of cannibalism using a discrete age-structured model of the adult and juvenile populations. Age-structured models with the inclusion of a prey in addition to the juvenile predators result in systems with three variables, see for example [3], as do models which use a separate variable for the total food resource [4].

It is possible to include intratrophic predation in two variable models without age-structure by representing the food available as a weighted sum of the prey and predator populations. In [5] Kohlmeier and Ebenhöh extend a cannibalistic model to cover intratrophic predation, which is applicable where the biological units are not individual species but aggregates of species within which predatory links are significant. The differential system they consider is

$$\dot{x} = x\left(\beta - \epsilon x - \frac{\alpha y}{1+\frac{x+\eta y}{H}}\right), \quad \dot{y} = y\left(\frac{\alpha'(x+\eta y) - \alpha\eta y}{1+\frac{x+\eta y}{H}} - \delta\right), \qquad (2)$$

where all parameters except η are positive, $\eta \geq 0$ and $\alpha' < \alpha$. They explain some unexpected observations in a large ecosystem model [6] by demonstrating that intratrophic predation by the predator not only stabilizes the system and increases the prey population, but also increases the predator population in some situations. Pitchford and Brindley [7] present a technique for incorporating intratrophic predation into two variable predator-prey models in general and demonstrate their approach by reference to (2).

We will show that (2) can be transformed to a system of the form

$$\begin{aligned}\dot{x} &= \lambda x + y + kxy,\\ \dot{y} &= -x + \lambda y + a_1x^2 + a_2xy + a_3y^2 + a_4x^3 + a_5x^2y + a_6xy^2 + a_7y^3,\end{aligned} \qquad (3)$$

where $a_i, k, \lambda \in \Re$. When $\lambda = 0$ this system is derived from a second order scalar equation and it has an invariant line, $kx = -1$. System (3) with $k = 0$ (known as the *Kukles* system) has been studied extensively, see for example [8], [9] and [10]. The behaviour of (3) when $k \neq 0$ is explored in some detail in [11].

Critical points are significant features of models represented by (1) as the populations are in equilibrium at such points. For completeness we recall that a critical point satisfies $P = Q = 0$ and its type is determined as follows. Let $\Delta = P_xQ_y - P_yQ_x$, $\vartheta = P_x + Q_y$ and $\rho = \vartheta^2 - 4\Delta$, where subscripts denote partial differentiation. These quantities are evaluated at the critical point. The

critical point is *degenerate* if $\Delta = 0$. It is a *saddle point* if $\Delta < 0$, a *node* if $\Delta > 0$ and $\rho \geq 0$, and a *focus* if $\Delta > 0, \rho < 0$ and $\vartheta \neq 0$. A node or focus is linearly stable if $\vartheta < 0$.

A critical point is a *centre* if all orbits in its neighbourhood are closed, whereas a *limit cycle* is an isolated closed orbit. If a non-degenerate critical point is a centre then certainly $\vartheta = 0$ (and $\Delta > 0$ necessarily), but this is far from sufficient. If $\vartheta = 0$ and the critical point is not a centre, it is said to be a *fine focus.* We shall say that a critical point is of *focus type* if it is a focus, a fine focus or a centre.

In both [5] and [7] the effect of changes in the parameter values on the position and linear stability of critical points that are nodes for (2) is considered. We extend the analysis to cover the stability of critical points that are fine foci; this requires consideration of the nonlinear terms in the differential equations representing the model. Deriving the conditions under which a critical point is a centre is a significant, and often difficult, problem which has attracted much attention and is the question that stimulates much of the interest in the Kukles system (to which we refer above). The centre conditions are required in order to investigate the bifurcation of limit cycles from a critical point and in the discussion of stability. In terms of the model the existence of centres and limit cycles can lead to multiple steady states.

In section 2 we outline the background to the techniques we will use in the analysis of system (2) and in section 3 we give details of the derivation of the system of equations (2). Sections 4 and 5 contain our analysis of the transformed system and the results in relation to the model. We show that at most one critical point of focus type can exist in the first quadrant: for the model this point cannot be a centre but it can be a fine focus surrounded by at most two limit cycles. Our conclusions are contained in section 6.

2 Mathematical background

Suppose that P and Q are analytic and suppose, without loss of generality, that the origin is a critical point. If the critical point at the origin is non-degenerate and of focus type then there are coordinates in terms of which the system takes the form

$$\dot{x} = \lambda x + y + p_2(x, y) + ..., \quad \dot{y} = -x + \lambda y + q_2(x, y) + ..., \tag{4}$$

where p_k, q_k are homogeneous polynomials of degree k. The degree of system (4) is that of the highest degree monomial present. If the origin is a centre then $\lambda = 0$ and there is an analytic first integral; the system is then sometimes described as being *integrable.*

We obtain the necessary conditions for the critical point at the origin to be a centre by calculating the *focal values*, which are polynomials in the coefficients arising in P and Q. There is a function V, analytic in a neighbourhood of the origin, such that its rate of change along orbits, $\dot{V}$, is of the form $\mu_2 r^2 + \mu_4 r^4 + ...$, where $r^2 = x^2 + y^2$ and the μ_{2k} are the focal values. Further details can be found in [12], for example. The stability of the critical point is determined by the sign of the first non-zero focal value.

For a given system there are infinitely many focal values, all of which must be zero for the origin to be a centre. By the Hilbert Basis Theorem the set of focal values has a finite basis, but the number of focal values making up this basis is not known *a priori*. We use the computer algebra procedure FINDETA [13] to calculate the first few focal values. Each of these is then expressed modulo the ideal generated by the previous ones; that is the relations $\mu_2 = \mu_4 = \ldots = \mu_{2k} = 0$ are used to eliminate some of the variables in μ_{2k+2}. The reduced focal value μ_{2k+2}, with strictly positive factors removed, is known as the *Liapunov quantity* $L(k)$. The circumstances under which the calculated $L(k)$ are zero simultaneously yield necessary centre conditions; the sufficiency of these conditions is proved independently. The origin is a fine focus of *order* k if $L(i) = 0$ for $i = 0, 1, \ldots, k-1$ and $L(k) \neq 0$. At most k small amplitude limit cycles can bifurcate out of a fine focus of order k and the sign of the first non-zero $L(k)$ determines the stability of the origin. We note that for system (4), $L(0) = \lambda$.

Various methods are used to prove the sufficiency of the centre conditions; in this paper we need only one of them, that is a search for an *integrating factor*. If the origin is of focus type then it is a centre if there is a function D such that

$$\frac{\partial}{\partial x}(DP) + \frac{\partial}{\partial y}(DQ) = 0$$

in a neighbourhood of the origin. Such a function is called an integrating factor or *Dulac function*. We make a systematic search for an integrating factor of the form $D = \prod_{i=1}^{n} C_i^{\alpha_i}$, where each $C_i = 0$ is an invariant algebraic curve. In this context, a function C is invariant with respect to system (4) if $\dot{C} = CL$, where L is a polynomial whose degree is at most one less than the degree of the system. The α_i and the coefficients in the C_i are functions of the coefficients in P, Q. The INVAR suite of programs which we use as an aid in the search for Dulac functions is described in [14].

3 A predator-prey system

We summarise the derivation of system (2) given by Pitchford and Brindley in [7]. Let $x \geq 0$ represent the prey and $y \geq 0$ the predator. The hypotheses

of the model are as follows:

(1) The specific grazing rate for y is $g(X)$, an increasing function of the food available (X) to the predators, which is zero when no food is available.

(2) The specific rate of higher predation ('external mortality') on y is $\gamma h(y)$, where h is a positive, increasing (or constant) function of y.

(3) In the absence of y, the prey growth rate, $A(x)$, is of a general logistic form. This may be interpreted as incorporating some form of environmental carrying capacity ($x = x_{max}$) into the model.

(4) The trivial equilibrium $(x_{max}, 0)$ must be unstable, so that prey and predator can coexist. This condition is satisfied if $g(x_{max}) - h(0) > 0$.

The model differs from a standard predator-prey model in that the food available to the predator is a linear combination of both the prey and predator densities, that is

$$X = x + \eta y, \ 0 \leq \eta \leq 1.$$

Thus η measures the amount of intratrophic predation in the predator population; $\eta = 1$ corresponds to the predator grazing indiscriminately on predator and prey alike. It is supposed that the effect of intratrophic predation is small, so that $\eta \ll 1$.

The ordinary differential equation representation of the population dynamics is derived as follows:

$$\begin{aligned}
\dot{x} &= (\text{growth rate of } x) - \ (\text{grazing rate of } y \text{ on } x) \\
&= A(x) - \frac{x}{(x+\eta y)} y g(x+\eta y), \\
\dot{y} &= \gamma(\text{total grazing rate of } y) - (\text{external mortality rate}) \\
&\quad -(\text{loss rate due to intratrophic predation}) \\
&= \gamma y g(x+\eta y) - \gamma y h(y) - \eta \frac{y}{(x+\eta y)} y g(x+\eta y) \\
&= y g(x+\eta y) \left(\gamma - \eta \frac{y}{(x+\eta y)} \right) - \gamma y h(y).
\end{aligned}$$

The condition $\gamma < 1$ is imposed so that γ is a measure of the inefficiency of conversion of food into predator reproduction. As we require $x \geq 0, y \geq 0$, the behaviour of the system in the first quadrant is relevant.

Pitchford and Brindley use system (2) to illustrate their approach. Let $A(x) = x(\beta - \epsilon x)$, $g(X) = \frac{\alpha X}{1+\frac{X}{H}}$, $h(y) = \frac{\alpha\delta}{\alpha'}$ and $\gamma = \frac{\alpha'}{\alpha}$, where $X = x + \eta y$, then the Pitchford and Brindley model becomes (2).

System (2) is non-dimensionalised in [5] with time in units of $\frac{1}{\beta}$, x in units of H and y in units of $\frac{\alpha'}{\alpha}H$ to give:

$$\dot{x} = x\left(1 - \epsilon x - \frac{\xi y}{(1 + x + \eta y)}\right), \quad \dot{y} = y\left(\xi\frac{(x - \kappa\eta y)}{(1 + x + \eta y)} - \delta\right), \tag{5}$$

where ϵ represents the logistic growth limitation of prey x, ξ predation intensity, δ mortality of predator y, κ uptake effect due to intratrophic predation and η is the intratrophic predation parameter. Again all parameters are positive, except η, which is non-negative. Assumption 4 is satisfied if $\frac{\xi}{1+\epsilon} - \delta > 0$.

Kohlmeier and Ebenhöh [5] studied (5) numerically and observed that intratrophic predation has a stabilizing effect: for specific parameter values the model exhibits a limit cycle when $\eta = 0$, but making $\eta > 0$ destroys the limit cycle. In this paper we show analytically that, when $\eta = 0$, the system can have no more than one bifurcating limit cycle (and hence an oscillatory stable state) surrounding the only critical point of focus type in the first quadrant. In contrast, under the conditions for which this limit cycle exists, but with $\eta > 0$, there are no bifurcating limit cycles surrounding the critical point. Moreover we determine the conditions under which the model, with $\eta > 0$, can have up to two bifurcating limit cycles.

4 Analysis of the system

Consider the possible critical points (steady states) for system (5), in which all parameters are non-negative. Clearly the origin is a critical point. When $x = 0$ (with $y \neq 0$) we have $y = \frac{-\delta}{\eta(\xi\kappa+\delta)} < 0$; this point is a saddle point and is not in the first quadrant. When $y = 0$ and $x \neq 0$ then $1 - \epsilon x = 0$. Further investigation shows that the origin and $(\frac{1}{\epsilon}, 0)$ are saddle points.

When $xy \neq 0$ we have $\dot{x} = 0$, $\dot{y} = 0$ if

$$-\xi y - \epsilon\eta xy - \epsilon x^2 - \epsilon x + \eta y + x + 1 = 0, \tag{6}$$

$$-\xi\eta\kappa y + \xi x - \delta\eta y - \delta x - \delta = 0. \tag{7}$$

Solving (6) and (7) simultaneously gives at most two critical points that do not lie on an axis. There are values of the parameters for which there is a critical point in the first quadrant provided that $\xi - \delta > 0$. If there are no such critical points there are no bifurcating limit cycles in the first quadrant. Henceforth we consider parameter ranges for which there is a critical point in the first quadrant and scale coordinates so that it is at $(1, 1)$. Then

$$\xi = (2 + \eta)(1 - \epsilon), \;\; \delta = (1 - \eta\kappa)(1 - \epsilon). \tag{8}$$

We require all parameters to remain positive so we must have $\epsilon < 1$ and $\eta\kappa < 1$. The critical point $(1,1)$ can be a focus or a node. The second critical point is at $\left(\frac{-\epsilon\eta\kappa+\epsilon-1}{\epsilon\eta(\kappa+1)}, \frac{-\epsilon\eta\kappa+\epsilon-\eta\kappa-\eta-1}{\epsilon\eta^2(\kappa+1)(2\kappa+1)}\right)$. For this point to be in the first quadrant we require $-\epsilon\eta\kappa+\epsilon-1>0$ and $-\epsilon\eta\kappa+\epsilon-\eta\kappa-\eta-1>0$. These can only be satisfied if $\epsilon-1>0$, whence $\xi<0$, which is a contradiction. In fact this critical point is a saddle point.

We conclude that there can be only one critical point with strictly positive coordinates.

Lemma 1 *System* (5) *has at most one critical point inside the first quadrant.*

Lemma 2 *The scaled system* (5) *has a critical point at* $(1,1)$*. There are parameter ranges for which it is a focus.*

Proof. We have seen in the above that there can only be one critical point in the first quadrant. Scaling such that this critical point is at $(1,1)$ we find that

$$\Delta = (\eta+2)(\epsilon-1)(\epsilon(1-2\eta\kappa-\eta)-1), \quad \vartheta = \eta(2\epsilon\kappa-2\kappa-1)-3\epsilon+1.$$

To maintain the positivity of ξ we require $\epsilon<1$, hence $\Delta>0$. There are non-negative values of the parameters such that $\rho=\vartheta^2-4\Delta<0$; the critical point can be of focus type. It is a fine focus when $\vartheta=0$. ■

We investigate the possibility that the critical point at $(1,1)$ for the scaled system can be either a centre or a focus surrounded by limit cycles. After a scaling of time by $1+x+\eta y$, (5) becomes

$$\begin{aligned}\dot{x} &= x(1+x-\epsilon x-2y+2\epsilon y+\epsilon\eta y-\epsilon x^2-\epsilon\eta xy),\\ \dot{y} &= y(s-u+ux-sy),\end{aligned} \tag{9}$$

where $s=\eta(1+2\kappa)(1-\epsilon), u=(1+\eta+\eta\kappa)(1-\epsilon)$. We transform (9) to canonical form with the origin at $(1,1)$. The new origin is a fine point if $s+3\epsilon+\epsilon\eta=1$ and it is a focus if $\sigma^2=-2\epsilon u-s^2+2u>0$. Clearly we must have $u\neq 0$, else $\sigma^2\leq 0$. Let

$$x = 1+\frac{\sigma\tilde{x}+s\tilde{y}}{\sigma u}, \quad y = 1+\frac{\tilde{y}}{\sigma}$$

and scale time by σ^{-1}. Then

$$\begin{aligned}\dot{\tilde{x}} &= -\tilde{y}+a_1\tilde{x}^2+a_2\tilde{x}\tilde{y}+a_3\tilde{y}^2+a_4\tilde{x}^3+a_5\tilde{x}^2\tilde{y}+a_6\tilde{x}\tilde{y}^2+a_7\tilde{y}^3,\\ \dot{\tilde{y}} &= \tilde{x}+\frac{1}{\sigma}\tilde{x}\tilde{y},\end{aligned} \tag{10}$$

where

$$a_1 = \frac{s-\epsilon}{\sigma u},\ a_2 = \frac{2s^2 - 2\epsilon s + 5\epsilon u - 3u}{\sigma^2 u},\ a_3 = \frac{s(s^2 - \epsilon s + 5\epsilon u + su - 3u)}{\sigma^3 u},$$
$$a_4 = \frac{-\epsilon}{\sigma u^2},\quad a_5 = \frac{-3\epsilon s + 3\epsilon u + su - u}{\sigma^2 u^2},\ \ a_6 = \frac{-s(3\epsilon s - 6\epsilon u - 2su + 2u)}{\sigma^3 u^2},$$
$$a_7 = \frac{s^2(-\epsilon s + 3\epsilon u + su - u)}{\sigma^4 u^2}.$$

Clearly this system is of the form (3).

We use FINDETA to calculate the focal values for system (10) and hence determine the Liapunov quantities. Recall that strictly positive factors are removed from the Liapunov quantities and that $u \neq 0$ if the origin is of focus type. We have

$$L(0) = 1 - s - 3\epsilon - \epsilon\eta.$$

The origin is a fine focus of order at least one, or it is a centre, if $L(0) = 0$.

Consider first $\epsilon = 0$. To satisfy $L(0) = 0$ we must have $s = 1$. Then $\sigma^2 = 2u-1$ and system (10) becomes the quadratic system

$$\begin{aligned}\dot{\tilde{x}} &= -\tilde{y} + \frac{1}{\sigma u}\tilde{x}^2 - \frac{(3u-2)}{u(2u-1)}\tilde{x}\tilde{y} - \frac{1}{\sigma u}\tilde{y}^2,\\ \dot{\tilde{y}} &= \tilde{x} + \frac{1}{\sigma}\tilde{x}\tilde{y}.\end{aligned} \tag{11}$$

Using the technique described in [14] we find functions that are invariant with respect to (11). We can then construct a Dulac function and prove that the origin is a centre in this case. The centre conditions for quadratic systems in general are well known.

Lemma 3 *Suppose that $\epsilon = 0$, $s = 1$, $\sigma^2 = 2u - 1 > 0$. The origin is a centre for system* (10).

Proof. There is a function

$$D = \left(1 + \frac{\tilde{y}}{\sigma}\right)^{\alpha_1} \left(1 + \frac{\tilde{x}}{u} + \frac{\tilde{y}}{\sigma u}\right)^{\alpha_2},$$

where $\alpha_1 = \frac{2u}{1-2u}$, $\alpha_2 = \frac{3u-2}{1-2u}$, such that

$$\frac{\partial}{\partial\tilde{x}}\left(D\dot{\tilde{x}}\right) + \frac{\partial}{\partial\tilde{y}}\left(D\dot{\tilde{y}}\right) = 0.$$

Hence the origin is a centre. ■

We assume from now on that $\epsilon u \neq 0$ and let $\eta = \frac{1-s-3\epsilon}{\epsilon}$. The origin is a fine focus of order at least one or it is a centre. We calculate from μ_4 that

$$L(1) = u(Au + B),$$

where

$$\begin{aligned} A &= -2\epsilon^3 + 3\epsilon^2 s + 8\epsilon^2 + \epsilon s^2 + 2\epsilon s - 6\epsilon + s^2 - s, \\ B &= 2\epsilon s(-2\epsilon^2 - 4\epsilon s + 2\epsilon - s^2 + 2s). \end{aligned}$$

We note that when $\eta = 0$, by definition $s = 0$ also, so $B = 0$ and $A \neq 0$ if $L(0) = 0$. Hence $L(1) \neq 0$; so the origin is a fine focus of maximum order one and it cannot be a centre. At most one limit cycle can be bifurcated from the critical point when $\eta = 0$.

Assume for the time being that $A \neq 0$. Let $u = -B/A$; then $L(1) = 0$. To maintain $\sigma^2 > 0$ we must have $u \neq 0$, so $B \neq 0$ also. Now the origin is a fine focus of order at least two or it is a centre. For a fine focus of order three or more we require $\mu_6 = 0$, that is

$$\epsilon s A(3\epsilon + s - 1)(2\epsilon + s)(\epsilon + s - 1)\Theta = 0,$$

where

$$\Theta = -3\epsilon^3 + 2\epsilon^2 s + 12\epsilon^2 + \epsilon s^2 + 10\epsilon s - 9\epsilon + s^2 - 4s.$$

We must have $\sigma^2 = \frac{-sC(2\epsilon+s)(\epsilon+s-1)}{A} > 0$, where

$$C = 4\epsilon^2 + \epsilon s - 4\epsilon + s.$$

In particular, therefore, $sC(2\epsilon + s)(\epsilon + s - 1) \neq 0$ and

$$L(2) = -\epsilon C(3\epsilon + s - 1)\Theta.$$

When $3\epsilon + s = 1$, then $\eta = 0$ and $s = 0$ also; hence $\sigma = 0$.

Consider $\Theta = 0$, with $ABC(2\epsilon + s)(\epsilon + s - 1)(3\epsilon + s - 1) \neq 0$. Substituting $u = -B/A$ into the focal values μ_8, μ_{10} gives

$$L(3) = -\epsilon A s(3\epsilon + s - 1)\Phi, \quad L(4) = \epsilon C(3\epsilon + s - 1)\Gamma,$$

where Φ, a polynomial of degree 17 in ϵ and degree 12 in s, and Γ, which is of degree 31 in ϵ and 22 in s, are in the Appendix. By calculating resultants to eliminate s, we find that $\Theta = \Phi = 0$ if

$$\epsilon(\epsilon^2-1)(\epsilon-3)(9\epsilon^2-1)(4\epsilon-3)(\epsilon^2-10\epsilon+5)(4\epsilon^2-11\epsilon+3)(7\epsilon^2-7\epsilon+4)\Psi = 0, \quad (12)$$

where

$$\Psi = \epsilon^4 + 9\epsilon^3 - 53\epsilon^2 + 31\epsilon - 4.$$

Similarly we calculate that $\Theta = \Gamma = 0$ if

$$\epsilon(\epsilon^2-1)(\epsilon-3)(9\epsilon^2-1)(4\epsilon-3)(\epsilon^2-10\epsilon+5)(4\epsilon^2-11\epsilon+3)(7\epsilon^2-7\epsilon+4)Z = 0, \quad (13)$$

where Z is an irreducible polynomial of degree 18 in ϵ. Substituting the values of ϵ, that satisfy (12) and (13) simultaneously, into $\Theta = 0, \Phi = 0, \Gamma = 0$, or by calculating resultants with respect to ϵ, we find corresponding values for s. With ϵ given by $\epsilon(\epsilon^2-1)(\epsilon-3)(\epsilon^2-10\epsilon+5)(4\epsilon^2-11\epsilon+3)(7\epsilon^2-7\epsilon+4) = 0$ all ϵ, s pairs satisfying $\Theta = \Phi = \Gamma = 0$ are such that $AB = 0$. Similarly $\sigma^2 \leq 0$, if $(9\epsilon^2-1)(4\epsilon-3) = 0$ with corresponding values for s. Hence, under current assumptions, we cannot have $L(2) = L(3) = L(4) = 0$ and there are no conditions under which the origin is a centre for (10). However, when $\Psi = 0$, $\Omega = s^4 - 38s^3 + 23s^2 + 12s - 4 = 0$, then $\Theta = \Phi = 0$ and $L(4) \neq 0$. The origin can be a fine focus of maximum order four in this case.

Lemma 4 *Suppose that* $\epsilon s \neq 0$, $1-s-3\epsilon-\epsilon\eta = 0$ *and* $\sigma^2 = -2\epsilon u - s^2 + 2u > 0$. *The origin is a fine focus of order at most four for system* (10).

Proof. When $1 - s - 3\epsilon - \epsilon\eta = 0$ and $\sigma^2 = -2\epsilon u - s^2 + 2u > 0$ the origin is a fine focus for system (10). We have shown that when $\epsilon s \neq 0$, there are no values of the coefficients in system (10) for which $L(i) = 0$, for $i = 0, 1, 2, 3, 4$. Hence the origin cannot be a fine focus of order greater than four. ■

Lemma 5 *Suppose that* $\epsilon s \neq 0$, $1 - s - 3\epsilon - \epsilon\eta = 0$, $\sigma^2 = -2\epsilon u - s^2 + 2u > 0$, $u = \frac{-2\epsilon s(-2\epsilon^2-4\epsilon s+2\epsilon-s^2+2s)}{A}$, $A = -2\epsilon^3 + 3\epsilon^2 s + 8\epsilon^2 + \epsilon s^2 + 2\epsilon s - 6\epsilon + s^2 - s \neq 0$, $\Psi = \epsilon^4 + 9\epsilon^3 - 53\epsilon^2 + 31\epsilon - 4 = 0$ *and* $\Omega = s^4 - 38s^3 + 23s^2 + 12s - 4 = 0$. *The origin is a fine focus of order four for system* (10).

Proof. When the conditions of Lemma 5 hold $L(0) = L(1) = L(2) = L(3) = 0$ and $L(4) \neq 0$. The origin is a fine focus of order four. ■

Corollary 6 *Up to four limit cycles can be bifurcated from the origin in system* (10) *when the conditions given in Lemma 5 hold.*

Proof. The origin is a fine focus of order four when the conditions of Lemma 5 hold. Then

$$\begin{aligned}
L(0) &= 1 - s - 3\epsilon - \epsilon\eta = 0,\\
L(1) &= u(Au + B) = 0,\\
L(2) &= -C(3\epsilon + s - 1)\Theta = 0,\\
L(3) &= -As(3\epsilon + s - 1)\Phi = 0,\\
L(4) &= C(3\epsilon + s - 1)\Gamma \neq 0,
\end{aligned}$$

where $A, B, C, \Theta, \Phi, \Gamma$ are as given above. Let ϵ^* be the unique root of $\Psi = 0$ in $I = (0.4570539979549, 0.45705399795495)$ and s^* the unique root of $\Omega = 0$

in $(0.850095, 0.850096)$. When $\epsilon = \epsilon^*, s = s^*$ we have $\Theta = 0, \Phi = 0, A < 0, B > 0, C < 0$ and $3\epsilon + s - 1 > 0$.

The stability of the origin is given by the sign of $L(4)$, which is the sign of $-\Gamma$. We use $\Theta = \Omega = 0$ to eliminate s from Γ. Then $\Gamma = \frac{27bN}{2(\epsilon+1)^{13}M}$, where $M = 10\epsilon^6 + 205\epsilon^5 + 913\epsilon^4 + 2567\epsilon^3 - 71\epsilon^2 - 836\epsilon + 220$ and N is a polynomial of degree 49 in ϵ. We find $M = 0$ and $N = 0$ have no roots in the interval I. Furthermore both M and N are positive for ϵ in I. We conclude that $\Gamma > 0$ when $\epsilon = \epsilon^*$, $s = s^*$. Hence $L(4) < 0$; the origin is stable.

We bifurcate limit cycles by successive perturbation of the parameters ϵ, s, u and η. At each perturbation the stability of the origin is reversed and a limit cycle bifurcates. Provided the perturbations are small enough existing limit cycles are not destroyed.

If we perturb ϵ, so that $L(3)$ becomes positive, the stability of the origin is reversed and a limit cycle bifurcates. The sign of $L(3)$ is the sign of $-\Phi$. We use $\Omega = \Theta = 0$ to eliminate s from Φ. Then $\Phi = \frac{27\epsilon\Psi\Upsilon}{2(\epsilon+1)^5 M}$, where Υ is a polynomial of degree 23 in ϵ. Here $\Upsilon = 0$ has no roots in I and $\Upsilon < 0$ in I. We decrease ϵ, so that Ψ becomes positive and hence $\Phi < 0$, $L(3) > 0$. We adjust s so that $\Theta = 0$ still holds and, provided that the perturbations are small enough so that all other conditions are still satisfied, a limit cycle is bifurcated.

Similarly we perturb s such that Θ becomes non-zero and $L(2) < 0$. When $\epsilon = \epsilon^*$, Θ is a quadratic in s with a positive leading coefficient and negative trailing coefficient. We decrease s, then $\Theta < 0$ and hence $L(2) < 0$. The stability of the origin is reversed and a second limit cycle is bifurcated.

A third limit cycle is bifurcated by increasing u so that $L(1)$ becomes positive and the stability of the origin is reversed. Again, provided that all the perturbations are small enough the other limit cycles are not destroyed.

Finally we increase η so that $L(0) < 0$. The stability of the origin is reversed and provided the perturbation is small enough the other three limit cycles persist. A fourth limit cycle is bifurcated. ■

We return to the possibility that $A = B = 0$, and hence $L(1) = 0$. We still assume that $\epsilon \neq 0$. When $s \neq 0$, then $A = B = 0$, if $\epsilon = 1$ and $s = -2$ or if $\epsilon^2 - 10\epsilon + 5 = 0$ and $s^2 + 30s - 20 = 0$. In either case the origin is no longer a focus. When $s = 0$, then $B = 0$ and $A = -2\epsilon(\epsilon - 1)(\epsilon - 3)$, $\sigma^2 = 2u(1 - \epsilon)$. The origin remains of focus type, with $A = B = 0$, only if $\epsilon = 3$; then the origin is a centre.

Lemma 7 *Let $s = 0$, $\epsilon = 3$, $\eta = -\frac{8}{3}$, $\sigma^2 = -4u > 0$. The origin is a centre for system* (10).

Proof. There exists a Dulac function

$$D = \left(1 + \frac{\tilde{y}}{\sigma}\right)^{\alpha_1} \left(1 + \frac{\tilde{x}}{u}\right)^{-3} e^{\alpha_2 \tilde{y}},$$

where $\alpha_1 = -\frac{u+2}{2}$, $\alpha_2 = -\frac{2\sigma}{u^2}$, such that

$$\frac{\partial}{\partial \tilde{x}}\left(D\dot{\tilde{x}}\right) + \frac{\partial}{\partial \tilde{y}}\left(D\dot{\tilde{y}}\right) = 0.$$

Consequently the origin is a centre for system (10). ■

We summarise the results of Lemmas 3, 4, 5, 7 and Corollary 6 for system (10) in the following two Theorems.

Theorem 8 *The origin is a centre for system* (10) *if and only if one of the following holds.*

(i) $\epsilon = 0$, $s = 1$, $\sigma^2 = 2u - 1 > 0$;

(ii) $s = 0$, $\epsilon = 3$, $\eta = -\frac{8}{3}$, $\sigma^2 = -4u > 0$.

Theorem 9 *Suppose that* $\epsilon s \neq 0$, $1 - s - 3\epsilon - \epsilon\eta = 0$, $\sigma^2 = -2\epsilon u - s^2 + 2u > 0$. *The origin is a fine focus of order at most four for system* (10). *It is of order four when* $A = -2\epsilon^3 + 3\epsilon^2 s + 8\epsilon^2 + \epsilon s^2 + 2\epsilon s - 6\epsilon + s^2 - s \neq 0$, $u = \frac{-2\epsilon s(-2\epsilon^2 - 4\epsilon s + 2\epsilon - s^2 + 2s)}{A}$, $\Psi = \epsilon^4 + 9\epsilon^3 - 53\epsilon^2 + 31\epsilon - 4 = 0$ *and* $\Omega = s^4 - 38s^3 + 23s^2 + 12s - 4 = 0$. *Then four limit cycles can be bifurcated from the origin.*

5 Analysis for the model

In system (5) all the parameters are strictly positive, except η, which is non-negative. Assumption 4 of the model requires $\xi - \delta(1 + \epsilon) > 0$ and there is a critical point in the first quadrant if $\xi > \delta$. We can satisfy these requirements in the scaled system (10) if we maintain $\kappa > 0$, $0 < \epsilon < 1$, $0 \leq \eta\kappa < 1$, and hence $u > 0$, $s \geq 0$. With these restrictions on the parameter values neither of the conditions of Theorem 8 can be satisfied; the origin cannot be a centre for system (10).

Lemma 10 *Suppose that* $\kappa > 0$, $0 < \epsilon < 1$, $0 \leq \eta\kappa < 1$. *The origin cannot be a centre for system* (10).

Proof. The origin is a centre for system (10) if and only if one of the conditions of Theorem 8 holds. Then the requirement that $0 < \epsilon < 1$ is not satisfied; the origin cannot be a centre. ■

Lemma 11 *Suppose that $\kappa > 0$, $0 < \epsilon < 1$, $0 \leq \eta\kappa < 1$. The origin cannot be a fine focus of order four for system* (10).

Proof. The origin is a fine focus of order four for system (10) when the conditions of Theorem 9 hold. In particular $\Psi = \epsilon^4 + 9\epsilon^3 - 53\epsilon^2 + 31\epsilon - 4 = 0$ and $\Omega = s^4 - 38s^3 + 23s^2 + 12s - 4 = 0$. The only root of $\Psi = 0$ that satisfies $0 < \epsilon < 1$ is in (0.186694,0.186695). The corresponding root of $\Omega = 0$ is negative. We require $s \geq 0$; the origin cannot be a fine focus of order four. ■

We demonstrate that for system (10), with $\kappa > 0$, $0 < \epsilon < 1$, $0 \leq \eta\kappa < 1$, the origin can be a fine focus of order two but no more and two limit cycles can be bifurcated from a fine focus of order two at the origin.

Theorem 12 *Suppose that $\kappa > 0$, $0 < \epsilon < 1$, $0 \leq \eta\kappa < 1$. The origin can be a fine focus of maximum order two for system* (10).

Proof. The origin is a fine focus for system (10) if $\sigma^2 = -s^2 + 2u(1-\epsilon) > 0$ and $s + 3\epsilon + \epsilon\eta = 1$, where $s = \eta(1+2\kappa)(1-\epsilon)$, $u = (1+\eta+\eta\kappa)(1-\epsilon)$. We must have $\epsilon < 1$, so with $\eta \geq 0$, $\kappa > 0$ we require $s \geq 0$, $u > 0$.

Consider first $\eta = 0$. By definition, $s = 0$ and for the origin to be a fine point we must have $\epsilon = \frac{1}{3}$. Then $u = \frac{2}{3}$ and $\sigma^2 = \frac{8}{9}$. The origin is a fine focus. When $s = 0$, $\epsilon = \frac{1}{3}$ then $B = 0$, $A < 0$ and hence $L(1) = Au^2 < 0$. The origin can be a fine focus of maximum order one and when it is of order one the origin is stable.

We assume from now on that $\eta > 0$ and hence $s > 0$. The origin is a fine point if $\eta = \frac{1-s-3\epsilon}{\epsilon}$; for $\eta > 0$ we require $s + 3\epsilon < 1$ and to maintain $s > 0$ we must have $3\epsilon < 1$. From the definition of s we have $\kappa = \frac{(1-\epsilon)(3\epsilon-1)+s}{2(1-s-3\epsilon)(1-\epsilon)}$ and $\kappa > 0$ if $s > (1-\epsilon)(1-3\epsilon)$. Replacing κ in u we have $\sigma^2 = \frac{-(\epsilon+s-1)(\epsilon s+(\epsilon-1)^2)}{\epsilon} > 0$ if $s + \epsilon < 1$, which is satisfied when $s + 3\epsilon < 1$. The origin is a fine focus if

$$0 < \epsilon < \frac{1}{3}, \quad (3\epsilon - 1)(\epsilon - 1) < s < 1 - 3\epsilon, \tag{14}$$

and it can be of order one.

The origin is a fine focus of order greater than one if $L(1) = u(Au + B) = 0$. With $u > 0$, this can only be satisfied if $AB < 0$. The sign of B is given by the sign of $D = -s^2+2(1-\epsilon)s+2\epsilon(1-\epsilon)$. The roots, s, of $D = 0$ are of opposite sign when $0 < \epsilon < \frac{1}{3}$. In particular the positive root $s_+ = 1 - 2\epsilon + \sqrt{2\epsilon^2 - 2\epsilon + 1} > 1 - 3\epsilon$. We conclude that $B > 0$ when ϵ, s satisfy (14). Similarly A, when viewed as a quadratic in s, has roots of opposite sign when $0 < \epsilon < \frac{1}{3}$. Here $s_+ = \frac{(1-3\epsilon)(\epsilon+1)+r}{2(\epsilon+1)}$, where $r^2 = (\epsilon+1)(17\epsilon^3 - 29\epsilon^2 + 19\epsilon + 1)$. As $s_+ > 1 - 3\epsilon$, when $0 < \epsilon < \frac{1}{3}$, we have $A < 0$ for ϵ, s satisfying (14). The origin can be a fine focus of order two for (10).

The origin is a fine focus of order three if and only if $\Theta = 0$. Consider Θ as a quadratic in s. For $0 < \epsilon < \frac{1}{3}$ there is only one positive root of $\Theta = 0$, this is $s_+ = \frac{-2(\epsilon^2+5\epsilon-2)+r}{2(b+1)}$, where $r^2 = 4(4\epsilon^4 + \epsilon^3 + 18\epsilon^2 - 11\epsilon + 4)$. However, when $0 < \epsilon < \frac{1}{3}$ then $s_+ > 1 - 3\epsilon$ and $\Theta < 0$. The origin cannot be a fine focus of order three and the maximum order of the origin as a fine focus is two. ■

Lemma 13 *Suppose that* $\kappa > 0$, $0 < \epsilon < \frac{1}{3}$, $0 \leq \eta\kappa < 1$, $1 - s - 3\epsilon - \epsilon\eta = 0$, $(3\epsilon - 1)(\epsilon - 1) < s < 1 - 3\epsilon$, $\sigma^2 = -2\epsilon u - s^2 + 2u > 0$, $u = \frac{-B}{A} > 0$, $A = -2\epsilon^3+3\epsilon^2 s+8\epsilon^2+\epsilon s^2+2\epsilon s-6\epsilon+s^2-s \neq 0$, $B = 2\epsilon s(-2\epsilon^2-4\epsilon s+2\epsilon-s^2+2s)$, $C = 4\epsilon^2 + \epsilon s - 4\epsilon + s \neq 0$. *The origin is a fine focus of order two for system* (10).

Proof. When the conditions of Lemma 13 hold $L(0) = 1 - s - 3\epsilon - \epsilon\eta = 0$, $L(1) = Au + B = 0$, $L(2) = -C(3\epsilon + s - 1)\Theta \neq 0$ and $\sigma^2 > 0$. The origin is a fine focus of order two. ■

Corollary 14 *Up to two limit cycles can be bifurcated from the origin in system* (10) *when the conditions given in Lemma 13 hold.*

Proof. The origin is a fine focus of order two for system (10) when the conditions given in Lemma 13 hold. Then

$$\begin{aligned} L(0) &= 1 - s - 3\epsilon - \epsilon\eta = 0, \\ L(1) &= Au + B = 0, \\ L(2) &= -C(3\epsilon + s - 1)\Theta \neq 0, \end{aligned}$$

where A, B, C, Θ are as given above. For $0 < \epsilon < \frac{1}{3}$, $(3\epsilon-1)(\epsilon-1) < s < 1-3\epsilon$ we have $\Theta < 0$, as shown in the proof of Lemma 12, and $3\epsilon + s - 1 < 0$. The sign of C determines the stability of the origin.

We have $C > 0$ when $s > \frac{4\epsilon(1-\epsilon)}{1+\epsilon}$ and vice versa. Let ϵ_1 be the unique root of $3\epsilon^2+6\epsilon-1 = 0$ in $(0.15470, 0.15471)$ and ϵ_2 be the unique root of $\epsilon^2-6\epsilon+1 = 0$ in $(0.171572, 0.171573)$. Then $C > 0$ for $0 < \epsilon < \epsilon_1$ and for $\epsilon_1 < \epsilon < \epsilon_2$ when $\frac{4\epsilon(1-\epsilon)}{1+\epsilon} < s < 1 - 3\epsilon$. Similarly, $C < 0$ for $\epsilon_2 < \epsilon < \frac{1}{3}$ and for $\epsilon_1 < \epsilon < \epsilon_2$ when $(3\epsilon - 1)(\epsilon - 1) < s < \frac{4\epsilon(1-\epsilon)}{1+\epsilon}$. We note that $C = 0$ when $s = \frac{4\epsilon(1-\epsilon)}{1+\epsilon}$, then $\sigma^2 = 0$ and the origin is no longer a focus.

We perturb u so that $(Au + B)L(2) < 0$; the stability of the origin is reversed and a limit cycle bifurcates. If $C > 0$ we increase u, else we decrease u. Next we perturb η such that $(Au + B)(1 - s - 3\epsilon - \epsilon\eta) < 0$. If $C > 0$ we decrease η, otherwise we increase η; the stability of the origin is reversed and a second limit cycle is bifurcated. Provided the perturbations are small enough the first limit cycle persists. ■

In summary we have the following result for system (2).

Theorem 15 *For system* (2) *there can be only one critical point in the first quadrant and it cannot be a centre. It can be a fine focus of maximum order two. Up to two limit cycles can be bifurcated from this fine focus.*

Proof. We have shown that, without loss of generality, system (2) can be transformed to system (10). The proof of Theorem 15 follows from the results contained in Lemmas 1, 2, 13, Theorem 12 and Corollary 14. ■

6 Conclusion

We have analysed system (10) which can be used to represent a predator-prey model with intratrophic predation. We conclude that system (2) can have only one critical point of focus type in the first quadrant and this point cannot be a centre. For certain values of the parameters the critical point can be a fine focus from which limit cycles can bifurcate. The fine focus can be of maximum order two and up to two limit cycles can be bifurcated from it when $\eta \neq 0$.

We find that when $\eta = 0$, system (5) can have a critical point in the first quadrant at $(\frac{\delta}{\xi-\delta}, \frac{\xi-\epsilon\delta-\delta}{(\xi-\delta)^2})$; this is a fine point when $\delta = \frac{\xi(1-\epsilon)}{(1+\epsilon)}$. This critical point can be a fine focus of maximum order one from which one stable limit cycle can be bifurcated. Then the critical point is unstable and all orbits are attracted to the stable oscillatory state. However, when $\delta = \frac{\xi(1-\epsilon)}{(1+\epsilon)}$ and $\eta \neq 0$, in system (5), there can be a linearly stable critical point in the first quadrant but there cannot be a fine critical point if the non-negativity of the parameters is maintained. Hence no limit cycles can be bifurcated from the critical point for parameter values satisfying $\delta = \frac{\xi(1-\epsilon)}{(1+\epsilon)}$. In contrast without this restriction on δ, but with $\eta \neq 0$, there can be up to two bifurcating limit cycles.

In considering the stability of the critical points (steady states) Kohlmeier and Ebenhöh examined the case with $\epsilon = 0$ analytically, then using numerical simulation perturbed ϵ so that it became positive. Here we have considered the possible phase portraits when $\epsilon > 0$ analytically. When both ϵ and η are zero in system (5) then the only critical point in the first quadrant is an unstable node, it cannot be a fine point. When $\epsilon = 0$ there is a critical point in the first quadrant at $(\frac{\delta+\eta\kappa}{\xi-\delta-\eta\kappa-\eta}, \frac{1}{\xi-\delta-\eta\kappa-\eta})$, with $\xi - \delta - \eta\kappa - \eta > 0$. This critical point is a stable node if $\eta > \frac{\delta}{\delta+\kappa(\epsilon-1)}$ and $\delta + \kappa(\epsilon - 1) > 0$. It is a fine point if $\epsilon - \delta - \eta(\kappa + 1) = 0$. Scaling the system such that this fine critical point is at $(1, 1)$ and transforming the system to canonical form with the origin at the fine point we have system (11). This is a quadratic system for which the origin is known to be a centre; both predator and prey populations can be arbitrarily large. However $\epsilon = 0$ violates assumption 3 of the Pitchford and Brindley model, the prey growth rate is no longer of parabolic form but is

linearly increasing with x, so this result is not unexpected. When $\epsilon > 0$, we find that system (5) can have at most two bifurcating limit cycles. The critical point is stable/unstable according to the value of ϵ.

7 Appendix

$$
\begin{aligned}
\Phi = &-72960b^{17} - 61040b^{16}s + 1094400b^{16} - 84648b^{15}s^2 + 1738224b^{15}s \\
&- 7004160b^{15} + 163712b^{14}s^3 + 2504136b^{14}s^2 - 14910656b^{14}s + \\
&25098240b^{14} + 695244b^{13}s^4 + 734208b^{13}s^3 - 23751808b^{13}s^2 + \\
&61327808b^{13}s - 55595520b^{13} + 395370b^{12}s^5 - 4851932b^{12}s^4 - \\
&21548400b^{12}s^3 + 101724160b^{12}s^2 - 141209888b^{12}s + 79234560b^{12} \\
&- 282170b^{11}s^6 - 6777870b^{11}s^5 - 1898160b^{11}s^4 + 110074832b^{11}s^3 \\
&- 227370128b^{11}s^2 + 194020640b^{11}s - 72960000b^{11} - 396955b^{10}s^7 \\
&- 4439536b^{10}s^6 + 9663852b^{10}s^5 + 67175936b^{10}s^4 - 241418160b^{10}s^3 \\
&+ 285264720b^{10}s^2 - 160880064b^{10}s + 42024960b^{10} - 178391b^9s^8 - \\
&1999700b^9s^7 + 6754246b^9s^6 + 26888092b^9s^5 - 157073560b^9s^4 + \\
&270686096b^9s^3 - 203648704b^9s^2 + 77349056b^9s - 13789440b^9 - \\
&38415b^8s^9 - 675771b^8s^8 + 1951208b^8s^7 + 11020334b^8s^6 - \\
&67861824b^8s^5 + 152746824b^8s^4 - 161513040b^8s^3 + 78916160b^8s^2 - \\
&19039728b^8s + 1969920b^8 - 3647b^7s^{10} - 144798b^7s^9 + 181449b^7s^8 + \\
&4417936b^7s^7 - 22062534b^7s^6 + 51501632b^7s^5 - 70420464b^7s^4 + \\
&49546608b^7s^3 - 14448008b^7s^2 + 1665648b^7s - 32b^6s^{11} - 12995b^6s^{10} \\
&- 32703b^6s^9 + 1045519b^6s^8 - 4882686b^6s^7 + 10683238b^6s^6 - \\
&14921196b^6s^5 + 14772448b^6s^4 - 7164944b^6s^3 + 894120b^6s^2 + 12b^5s^{12} \\
&+ 650b^5s^{11} - 1848b^5s^{10} + 106794b^5s^9 - 482707b^5s^8 + 1052016b^5s^7 \\
&- 986718b^5s^6 + 776804b^5s^5 - 1113236b^5s^4 + 439088b^5s^3 + 144b^4s^{12} \\
&+ 2892b^4s^{11} + 8566b^4s^{10} - 20501b^4s^9 - 66605b^4s^8 + 246384b^4s^7 - \\
&488598b^4s^6 + 396630b^4s^5 - 33100b^4s^4 + 432b^3s^{12} + 3640b^3s^{11} - \\
&6067b^3s^{10} - 23922b^3s^9 + 83079b^3s^8 - 116096b^3s^7 + 116632b^3s^6 - \\
&61490b^3s^5 + 552b^2s^{12} + 860b^2s^{11} - 8891b^2s^{10} + 9035b^2s^9 + 3769b^2s^8 \\
&- 8383b^2s^7 + 3058b^2s^6 + 324bs^{12} - 1074bs^{11} - 678bs^{10} + 6822bs^9 \\
&- 8934bs^8 + 3540bs^7 + 72s^{12} - 504s^{11} + 1080s^{10} - 936s^9 + 288s^8,
\end{aligned}
$$

$$
\begin{aligned}
\Gamma =& 2737256448b^{31} + 7822136320b^{30}s - 71168667648b^{30} + 23215934464b^{29}s^2 \\
& - 2452138311168b^{29}s + 848549498880b^{29} + 8163648512b^{28}s^3 - \\
& 7287607142240b^{28}s^2 + 3332950986752b^{28}s - 6158827008000b^{28} - \\
& 771660236800b^{27}s^4 - 7848682967040b^{27}s^3 + 1007578588876 8b^{27}s^2 - \\
& 264906127114240b^{27}s + 304656642662400b^{27} - 154687413888b^{26}s^5 + \\
& 72994648780 8b^{26}s^4 + 15245259456512b^{26}s^3 - 813761463060480b^{26}s^2 \\
& + 139079421739008b^{26}s - 108970179194880b^{26} - 163051324864b^{25}s^6 + \\
& 30600941788160b^{25}s^5 + 6384615036416b^{25}s^4 - 1442027733790720b^{25}s^3 \\
& + 430501419680768b^{25}s^2 - 514515221569536b^{25}s + 291764164792320b^{25} \\
& - 3258825168b^{24}s^7 + 4981645919040b^{24}s^6 - 1573237965747 2b^{24}s^5 - \\
& 1388982504581120b^{24}s^4 + 8242920616099840b^{24}s^3 - 1586214386906112b^{24}s^2 \\
& + 1393327297646592b^{24}s - 5970777490022400b^{24} + 358408836360b^{23}s^8 + \\
& 45182405007040b^{23}s^7 - 42538891376320b^{23}s^6 - 4409892220928 0b^{23}s^5 + \\
& 10097756495621120b^{23}s^4 - 31327952211333120b^{23}s^3 + \\
& 42231145656944640b^{23}s^2 - 2826378374037504b^{23}s + 944846180720640b^{23} \\
& + 55529351712 8b^{22}s^9 + 100348750512b^{22}s^8 - 57674297974304b^{22}s^7 + \\
& 109000449981504b^{22}s^6 + 8297464260830720b^{22}s^5 - 4209327156626432b^{22}s^4 \\
& + 83347144506654720b^{22}s^3 - 83094651203020800b^{22}s^2 \\
& + 43502216259194880b^{22}s - 11613357931929600b^{22} + 308907235844b^{21}s^{10} - \\
& 5095149079480b^{21}s^9 - 453068432408480b^{21}s^8 + 240388753833184b^{21}s^7 + \\
& 3464593858245760b^{21}s^6 - 41946258463124480b^{21}s^5 + \\
& 11465199863188992b^{21}s^4 - 15991544834488320b^{21}s^3 + \\
& 12236503115492352b^{21}s^2 - 5104636768608256b^{21}s + 1106295040536576b^{21} \\
& - 86386398730b^{20}s^{11} - 6840556753272b^{20}s^{10} - 172641924476 56b^{20}s^9 + \\
& 2624692013594720b^{20}s^8 - 17631590590243200b^{20}s^7 - 3131087320096192b^{20}s^6 \\
& + 11972393965058816b^{20}s^5 - 21588810888840192b^{20}s^4 + \\
& 22491078269306880b^{20}s^3 - 13546050387758080b^{20}s^2 + \\
& 4553644603092992b^{20}s - 809083735412736b^{20} - 2572470162 32b^{19}s^{12} - \\
& 53425889182960b^{19}s^{11} + 2131155075312b^{19}s^{10} + 190855841969288b^{19}s^9 \\
& - 427926034246576b^{19}s^8 - 1666014313959072b^{19}s^7 + \\
& 98224675495363200b^{19}s^6 - 22126130227686400b^{19}s^5 + \\
& 28881023481622016b^{19}s^4 - 23328171999795200b^{19}s^3 + \\
& 1123442796444364 8b^{19}s^2 - 30535193319833600b^{19}s + \\
& 4458169576857 60b^{19} - 202631959417b^{18}s^{13} - 31040693397920b^{18}s^{12} \\
& + 6621260408556b^{18}s^{11} + 106689790907224b^{18}s^{10} - \\
& 3821301770469200b^{18}s^9 - 6068100772421280b^{18}s^8 + 6394230725726816b^{18}s^7 \\
& - 1782911726845254 4b^{18}s^6 + 27858435308439040b^{18}s^5 - \\
& 2773459501920563 2b^{18}s^4 + 17785607449509888b^{18}s^3 - \\
& 6895588975107072b^{18}s^2 + 1505337422897152b^{18}s - \\
& 179098689392640b^{18} - 97859799582b^{17}s^{14} - 1480824316673b^{17}s^{13} +
\end{aligned}
$$

$$41820140442666b^{17}s^{12} + 517173428090560b^{17}s^{11} - 2290528842903200b^{17}s^{10} - 1654442783355120b^{17}s^{9} + 3427820263024432b^{17}s^{8} - 11401261889378208b^{17}s^{7} + 2081724910006240 0b^{17}s^{6} - 24323277351511552b^{17}s^{5} + 1905905938584422 4b^{17}s^{4} - 98344682510028800b^{17}s^{3} + 30597505035909120b^{17}s^{2} - 5248131327344640b^{17}s + 495169691443200b^{17} - 33940207269b^{16}s^{15} - 5892824414240b^{16}s^{14} + 1501182170221b^{16}s^{13} + 228027437093920b^{16}s^{12} - 10463186709080400b^{16}s^{11} - 595833575165360b^{16}s^{10} + 16125086438904880b^{16}s^{9} - 58863010873536800b^{16}s^{8} + 120590060539166720b^{16}s^{7} - 161120611778012800b^{16}s^{6} + 146690846963161600b^{16}s^{5} - 9213456578890752b^{16}s^{4} + 384220327132364800b^{16}s^{3} - 9431217347287040b^{16}s^{2} + 1208722197012480b^{16}s - 84252753469440b^{16} - 9184050486b^{15}s^{16} - 1914139771310b^{15}s^{15} + 274388527790b^{15}s^{14} + 87606884861970b^{15}s^{13} - 3663403514675800b^{15}s^{12} - 396805855164240b^{15}s^{11} + 6873587787065760b^{15}s^{10} - 25063944311611760b^{15}s^{9} + 53940612842500800b^{15}s^{8} - 79290231564534720b^{15}s^{7} + 819568999690028800b^{15}s^{6} - 5953211274037248b^{15}s^{5} + 3023104576436736b^{15}s^{4} - 1014390527776768b^{15}s^{3} + 1887666905733120b^{15}s^{2} - 161248475381760b^{15}s + 6651533168640b^{15} - 2035573215b^{14}s^{17} - 503492529120b^{14}s^{16} - 245890167500b^{14}s^{15} + 27279435516440b^{14}s^{14} - 905853500507700b^{14}s^{13} - 2540125891160000b^{14}s^{12} + 25786422960398000b^{14}s^{11} - 8757754328181520b^{14}s^{10} + 1836409911130152 0b^{14}s^{9} - 27675311962385760b^{14}s^{8} + 31331075297524800b^{14}s^{7} - 2601192589182784b^{14}s^{6} + 15290899916945920b^{14}s^{5} - 6290734336931840b^{14}s^{4} + 1677972819394560b^{14}s^{3} - 216948112128000b^{14}s^{2} + 9001388943360b^{14}s - 369946918b^{13}s^{18} - 10966897407b^{13}s^{17} - 345748666500b^{13}s^{16} + 64499315863000b^{13}s^{15} - 1231547354870000b^{13}s^{14} - 116346684959130b^{13}s^{13} + 7997314707541000b^{13}s^{12} - 2398645973967840b^{13}s^{11} + 443763374013752 0b^{13}s^{10} - 59364634093213600b^{13}s^{9} + 6568184318646560b^{13}s^{8} - 618475745007968 0b^{13}s^{7} + 44024254474182400b^{13}s^{6} - 2137368529433600b^{13}s^{5} + 71783768742400 0b^{13}s^{4} - 15115139278848 0b^{13}s^{3} + 1077061736448 0b^{13}s^{2} - 52321317b^{12}s^{19} - 2026049220b^{12}s^{18} - 130512748150b^{12}s^{17} + 10716933744400b^{12}s^{16} + 643162829250b^{12}s^{15} - 357107022396800b^{12}s^{14} + 18731861838645 0b^{12}s^{13} - 4679021742548800b^{12}s^{12} + 572752503796560b^{12}s^{11} - 155918494674320b^{12}s^{10} - 43976373250808 0b^{12}s^{9} + 4859151011387200b^{12}s^{8} - 665080802694720b^{12}s^{7} - 13877450443584 0b^{12}s^{6} + 788092655232 0b^{12}s^{5} - 269328097587200b^{12}s^{4} + 52740769075200b^{12}s^{3} - 525034600b^{11}s^{20} - 30820060100b^{11}s^{19} - 3381864702 0b^{11}s^{18} + 967126522500b^{11}s^{17} + 7745110881200b^{11}s^{16} - 697134349273 0b^{11}s^{15} + 281864648133400b^{11}s^{14} - 48875744235950 0b^{11}s^{13} - 491292550523000b^{11}s^{12} + 413317594239600b^{11}s^{11} - 89490409328368 0b^{11}s^{10} + 10538448809512800b^{11}s^{9} - 73322346702288 0b^{11}s^{8} + 29140935609120 0b^{11}s^{7} - 677461651897600b^{11}s^{6} + 13684091996160b^{11}s^{5} - 1295122068480b^{11}s^{4} - 325068b^{10}s^{21} -$$

$$34818300b^{10}s^{20} - 671909224b^{10}s^{19} - 885066396b^{10}s^{18} +$$
$$20773792606b^{10}s^{17} - 70848892860b^{10}s^{16} + 148515279440b^{10}s^{15} +$$
$$234824776012b^{10}s^{14} - 4008450249375b^{10}s^{13} + 16328128161808b^{10}s^{12} -$$
$$3540141906038 0b^{10}s^{11} + 46470655088712b^{10}s^{10} - 383639546734 96b^{10}s^{9} +$$
$$19417157109584b^{10}s^{8} - 53597052241 60b^{10}s^{7} + 720387817408b^{10}s^{6} -$$
$$92275750784b^{10}s^{5} - 9216b^{9}s^{22} - 2475660b^{9}s^{21} - 95729536b^{9}s^{20} -$$
$$613040700b^{9}s^{19} + 3032890956b^{9}s^{18} + 42012455 86b^{9}s^{17} - 338658563 16b^{9}s^{16} +$$
$$1249553115 08b^{9}s^{15} - 777117762650b^{9}s^{14} + 3341702530245b^{9}s^{13} -$$
$$8358406584898b^{9}s^{12} + 12815960074944b^{9}s^{11} - 123982178391 84b^{9}s^{10} +$$
$$7546037512184b^{9}s^{9} - 26906412802 40b^{9}s^{8} + 4103120804 16b^{9}s^{7} +$$
$$1304413184b^{9}s^{6} - 80712b^{8}s^{22} - 8334108b^{8}s^{21} - 138116992b^{8}s^{20} +$$
$$25055274b^{8}s^{19} + 3358879256b^{8}s^{18} - 6987705598b^{8}s^{17} - 45973032 48b^{8}s^{16}$$
$$- 365387383 95b^{8}s^{15} + 4344581912 48b^{8}s^{14} - 14719850966 73b^{8}s^{13} +$$
$$2722355768240b^{8}s^{12} - 3119900979532b^{8}s^{11} + 2268116160152b^{8}s^{10} -$$
$$1028830096280b^{8}s^{9} + 265987573392b^{8}s^{8} - 23398425136b^{8}s^{7} - 323856b^{7}s^{22} -$$
$$16068804b^{7}s^{21} - 97835596b^{7}s^{20} + 584854602b^{7}s^{19} + 673655100b^{7}s^{18} -$$
$$7810687822b^{7}s^{17} + 66533137 62b^{7}s^{16} + 611258605 95b^{7}s^{15} -$$
$$2551632971 42b^{7}s^{14} + 5123940406 47b^{7}s^{13} - 6363768825 78b^{7}s^{12} +$$
$$5141280042 96b^{7}s^{11} - 2660925636 00b^{7}s^{10} + 841792469 04b^{7}s^{9} -$$
$$1436657802 4b^{7}s^{8} - 776160b^{6}s^{22} - 18995652b^{6}s^{21} + 991232b^{6}s^{20} +$$
$$503909028b^{6}s^{19} - 1376398992b^{6}s^{18} - 1412067811b^{6}s^{17} + 158946530 48b^{6}s^{16}$$
$$- 441753635 10b^{6}s^{15} + 7342963819 6b^{6}s^{14} - 8236499371 1b^{6}s^{13} +$$
$$6199425022 4b^{6}s^{12} - 2942471932 4b^{6}s^{11} + 7626157640b^{6}s^{10} - 66833780 8b^{6}s^{9}$$
$$- 1215360b^{5}s^{22} - 13156476b^{5}s^{21} + 62960280b^{5}s^{20} + 80674532b^{5}s^{19} -$$
$$1001532470b^{5}s^{18} + 2721458133b^{5}s^{17} - 3688035266b^{5}s^{16} + 210257707 8b^{5}s^{15}$$
$$+ 982780878b^{5}s^{14} - 2699774363b^{5}s^{13} + 2500297478b^{5}s^{12} - 1444266096b^{5}s^{11}$$
$$+ 397231652b^{5}s^{10} - 1280736b^{4}s^{22} - 3556932b^{4}s^{21} + 507372 56b^{4}s^{20} -$$
$$1197325 25b^{4}s^{19} - 2566046 0b^{4}s^{18} + 6404334 53b^{4}s^{17} - 1450586 0676b^{4}s^{16} +$$
$$1724083539b^{4}s^{15} - 1158312032b^{4}s^{14} + 320003519b^{4}s^{13} + 79430096b^{4}s^{12} -$$
$$5559102b^{4}s^{11} - 903312b^{3}s^{22} + 2069364b^{3}s^{21} + 14181894b^{3}s^{20} -$$
$$7219839 3b^{3}s^{19} + 130422498b^{3}s^{18} - 90759675b^{3}s^{17} - 56357784b^{3}s^{16} +$$
$$1898968 17b^{3}s^{15} - 1950593 10b^{3}s^{14} + 9946513 5b^{3}s^{13} - 2075723 4b^{3}s^{12} -$$
$$409536b^{2}s^{22} + 2334144b^{2}s^{21} - 2624100b^{2}s^{20} - 10911636b^{2}s^{19} +$$
$$4057287 6b^{2}s^{18} - 5723084 4b^{2}s^{17} + 3695979 6b^{2}s^{16} - 505518 0b^{2}s^{15} -$$
$$5858844b^{2}s^{14} + 2223324b^{2}s^{13} - 108000bs^{22} + 879960bs^{21} - 2649000bs^{20}$$
$$+ 3008160bs^{19} + 1455600bs^{18} - 7674600bs^{17} + 8488440bs^{16} - 4218000bs^{15}$$
$$+ 817440bs^{14} - 12600s^{22} + 126000s^{21} - 491400s^{20} + 1008000s^{19} -$$
$$1197000s^{18} + 831600s^{17} - 315000s^{16} + 50400s^{15}.$$

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