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A Model for Lions-Hyenas Interactions

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Abstract

Competition is known in biology through various mechanisms and species often compete for resources indirectly. We consider a system consisting of a predator, prey, which is not fully consumed and converts to a secondary resource (carcasses), and scavengers, which feed on the carcasses. Such an ecosystem is a simplified sketch of interactions in the savannah between lions and spotted hyenas, with lions killing herbivore prey, whose leftovers serve as primary food for the hyenas. We perform an analytic and numerical study of the possible bifurcations which the model presents between states where one or more species are absent and the coexistence state.

Keywords: predator-prey dynamics, trophic chain, apparent competition, scavenging, feedback

MSC Classification: 92D40 , 34A34 , 34C23

1 Introduction

The motivation of this paper is the study of indirect competition of resources for a particular ecosystem. Competition is known in biology through various mechanisms. At the same trophic level, it damages both interacting species, either directly or through an intermediate agent. Sharing pastures, den or hunting locations causes friction among individuals of different populations [1–3], ultimately contributing to a reduction of the respective population sizes, up to possible complete eradication. Real competition is characterized by either interference between the single individuals, or exploitation. In the latter case, the intermingling of a species with a different one for feeding sites actually damages the weaker one or even both of them, [4]. The former consists in the disturbance action that the stronger individual exerts on the weaker one of another species. This is a common occurrence among herbivores, [5].

Another form of competition is more subtle, as it involves species neither directly interacting nor exploiting common resources, [6, 7]. The reciprocal interference occurs via an enemy, be it a predator or even a pathogen, that attacks both of them, [8, 9]. In the literature this is known as *apparent competition* [10]. An instance involves the squirrel pox virus which causes the fast death of red squirrels, but for which the grey squirrel is a healthy carrier, [11, 12].

In this paper we focus on mechanisms of competition and facilitation that characterise two top predators in the African savannah: lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) using mathematical modelling. The interactions are represented by a model ecosystem consisting of predators (lions), prey (herbivores), which is not fully consumed and converts to a secondary resource (carcasses), and scavengers (hyenas), which feed on the carcasses. The lions and hyenas are assumed to interact in two possible ways: lions kill hyenas, but do not eat them, and hyenas can interfere with lions at the lions' killing site to distract them from their prey, or can kill lion cubs. The predators, however, facilitate the scavengers by providing opportunities for kleptoparasitism and consuming parts of their kill. Thus, the ecosystem has the structure of a trophic chain where the consumers are subject to two-way competition due to their feeding and social behaviour.

Overall, the interactions between the lions and hyenas reveal a complex picture with costs and benefits for both species affecting their coexistence in multiple ways [13]. To shed light into the interplay of these factors, we study analytically the possible bifurcations that the model presents between states where one or more species are absent and the coexistence state, and provide numerical illustrations. In our analysis we consider two scenarios: without and with hyenas' interference on the lion population (Section 2 and Section 5 respectively). The model equilibria and bifurcation structures are studied through theoretical analysis and numerical simulation.

2 The basic model with the simple Holling Type-I functional response

The model variables represent the populations sizes at time $t \geq 0$ as follows: $L(t)$ lions, $P(t)$ whole prey set, $C(t)$ carcasses, $H(t)$ hyenas.

We assume that the prey are herbivores and all lump together in one single population P, which contains all the possible species on which the lions L can feed. After being killed, not the whole prey are consumed by the lions, so that some parts, representing the remaining carcasses C, are left for the hyenas H to feed upon. We do not assume hyenas to be active predators. It is possible that some carcasses left over remain, which eventually will be consumed by other animals or eventually disappear from the environment by natural decay.

Furthermore, we assume two types of negative feedback between the two consumer carnivore species: first, lions can occasionally kill the hyenas, but do not eat them except under starvation, but this peculiar eating habit is ignored in our models, while the hyenas can form large groups to mob and distract lions feeding on their kill and steal the carcass, or successfully kill lion cubs [14–16]. This last feature is examined in the model that specifically takes into account the hyenas interference. Specifically, the reasons why lions do not eat hyenas may be related to the co-evolution of both species as top predators, which has reduced the possibility of them hunting each other. On one hand, lions may not find hyenas appetizing because their diet mainly consists of decaying meat, and the hyena flesh is high in uric acid. On the other hand, lions may avoid the risks of pathogen transmission from the hyenas, which agrees with the general observation of the aversion of carnivores to feed upon the carcasses of other carnivore species [17]. The second feedback is assumed to be much weaker because hyena kleptoparasitism is more efficient when male lions are absent [14, 15], and also because of local-scale avoidance strategy between the two carnivore populations [18]. Hence, in our initial analysis we shall ignore the second feedback mechanism, and then compare the two scenarios.

The predator, prey and scavenger exhibit intraspecific competition in the model for resources or due to social behaviour. Lions kill each other quite frequently, while hyenas compete for their share of the carcasses [13]. Since we combine in the single variable P all prey, consisting mainly of herbivores, it is reasonable to assume that pasture sizes may impose a limitation on their growth, so that for the herbivores we also assume intraspecific competition.

The conversion of resources into population follows a simple Holling type-I functional response. The per-capita reproduction rates for the lions and hyenas are proportional to the size of their respective consumer resource while the prey follow a logistic-type growth law. Natural decomposition of the carcasses follows an exponential decay. The model parameters are listed in Table 1.

$$\frac{dL}{dt} = r_L LP - m_L L - aL^2 \tag{1a}$$

$$\frac{dP}{dt} = -gLP + r_P P - m_P P - bP^2 \tag{1b}$$

$$\frac{dC}{dt} = egLP - r_H CH - nC \tag{1c}$$

$$\frac{dH}{dt} = fr_H CH - m_H H - kHL - zH^2. \tag{1d}$$

Parameter	Definition
g	Rate of predation by lions
r_H	Rate of consumption of carcasses by hyenas
k	Rate of killing of hyenas by lions
m_L	Natural mortality rate, lions
m_H	Natural mortality rate, hyenas
m_P	Natural mortality rate, prey
r_L	Growth rate, lions
r_P	Growth rate, prey
n	Removal rate, carcasses
e	Conversion factor killed prey to carcasses
f	Conversion factor, hyenas
a	Intraspecific competition, lions
b	Intraspecific competition, prey
z	Intraspecific competition, hyenas
α	Interference of hyenas onto lions feeding on prey

Table 1 Parameter definitions.

The first equation for the lions states that they reproduce by feeding on the prey, die naturally but also through intraspecific competition, that in some cases means a real killing of each other.

The second equation describes the herbivores dynamics, subject to hunting by lions, reproduction and natural mortality, and possible intraspecific competition for resources.

The equation for the carcasses is the novelty of the model. They are the leftovers of the lions' meals, and are consumed by the scavenger hyenas. If the latter do not eat them completely, the remains are assumed to decay naturally in the environment.

Finally the fourth equation for the hyenas shows that they reproduce by consuming the carcasses, are subject to natural mortality and to the killing by lions, and compete with their fellows for resources.

3 Analysis of model (1)

Note that

$$r_P \geq m_P \tag{2}$$

in (1b) must hold to ensure that the populations do not converge to extinction. Otherwise, $\frac{dP}{dt}(t) < 0$ for all $P > 0$, implying extinction of the prey and entailing the disappearance in turn also of lions, carcasses and ultimately also hyenas. Hence the condition (2) will be assumed from now on.

3.1 Boundedness

From equation (1b), introducing a constant $\eta_P > 0$, we obtain the following estimates from above

$$\frac{dP}{dt} + \eta_P P \leq (\eta_P + r_P - m_P)P - bP^2 \leq \Gamma_P^{\max}$$

where the constant on the right represents the maximum value of the parabola $\Gamma_P(P) = P[\eta_P + r_P - m_P - bP]$, i.e.

$$\Gamma_P^{\max} = \frac{(\eta_P + r_P - m_P)^2}{4b}.$$

Thus, solving the previous differential inequality, we obtain

$$P(t) \leq P(0)\exp(-\eta_P t) + [1 - \exp(-\eta_P t)]\frac{\Gamma_P^{\max}}{\eta_P} \leq P^M \equiv \max\left\{P(0), \frac{\Gamma_P^{\max}}{\eta_P}\right\}.$$

This shows the boundedness for all $t \geq 0$ for the prey population,

$$P(t) \leq P^M. \tag{3}$$

We now consider equation (1a). Let $\eta_L > 0$. Using the bound (3) we have

$$\frac{dL}{dt} + \eta_L L \leq [r_L P^M + \eta_L - m_L]L - aL^2 = \Gamma_L(L) \leq \Gamma_L^{\max},$$

where $\Gamma_L^{\max}$ is the maximum of the parabola $\Gamma_L(L) = [r_L P^M + \eta_L - m_L - aL]L$,

$$\Gamma_L^{\max} = \frac{(r_L P^M + \eta_L - m_L)^2}{4a}.$$

Ultimately for a suitable L^M,

$$L(t) \leq L(0)\exp(-\eta_L t) + [1 - \exp(-\eta_L t)]\frac{\Gamma_L^{\max}}{\eta_L} \leq L^M \equiv \max\left\{L(0), \frac{\Gamma_L^{\max}}{\eta_L}\right\}. \tag{4}$$

The equation (1c) in turn yields

$$\frac{dC}{dt} \leq egL^M P^M - nC,$$

for which

$$C(t) \leq C(0)\exp(-nt) + [1 - \exp(-nt)]\frac{egL^M P^M}{n}$$

and ultimately

$$C(t) \leq C^M \equiv \max\left\{C(0), \frac{egL^M P^M}{n}\right\}. \tag{5}$$

Entirely similar considerations as for (1b) hold for (1d), leading to the differential inequality

$$\frac{dH}{dt} + \eta_H H \leq (\eta_H + fr_H C^M - m_H)H - zH^2 \leq \Gamma_H^{\max}$$

with

$$\Gamma_H^{\max} = \frac{(\eta_H + f r_H C^M - m_H)^2}{4z}.$$

Ultimately then

$$H(t) \le H^M \equiv \max\left\{ H(0), \frac{\Gamma_H^{\max}}{\eta_H} \right\}. \tag{6}$$

3.2 Equilibria feasibility

Only three equilibria are feasible for (1) apart from the origin E_0, namely the prey-only point $E_1 = (0, P_1, 0, 0)$, $P_1 = (r_P - m_P)b^{-1}$, the hyenas-free point $E_2 = (L_2, P_2, C_2, 0)$ and coexistence E_*. Feasibility of E_1 is guaranteed by (2).

The population values at both equilibria E_2 and E_* can be explicitly evaluated. Namely, solving in turn equations (1a)-(1b) at equilibrium we find

$$P_2 = \frac{g m_L + a(r_P - m_P)}{\delta}, \quad L_2 = \frac{1}{\delta}\left[r_L(r_P - m_P) - b m_L\right], \quad \delta = g r_L + ab > 0. \tag{7}$$

Substituting into the third one, we get

$$C_2 = \frac{eg}{n} L_2 P_2,$$

which explicitly becomes

$$C_2 = \frac{eg}{n} \frac{g m_L + a(r_P - m_P)}{\delta^2}\left[r_L(r_P - m_P) - b m_L\right].$$

This equilibrium is feasible if $L_2 \ge 0$ which entails

$$r_P - m_P \ge \frac{b m_L}{r_L} \ge 0, \tag{8}$$

implying also the nonnegativity of P_2 and in turn the one of C_2.

At coexistence, the values of the first two populations do not change with respect to those of the previous equilibrium,

$$P_* = P_2, \quad L_* = L_2.$$

Hence condition (8) is needed also for the feasibility of E_*.

Setting (1d) at equilibrium, we obtain

$$H = \frac{1}{z}[f r_H C - (m_H + k L_2)], \tag{9}$$

and at equilibrium (1c) upon substitution gives the quadratic

$$\Pi(C) = \pi_2 C^2 + \pi_1 C + \pi_0 = 0, \quad \pi_2 = f r_H^2 > 0, \quad \pi_0 = -egz L_2 P_2 < 0,$$

and

$$\pi_1 = nz - r_H(m_H + kL_2).$$

But π_2 and π_0 being opposite in sign guarantee the existence of a unique positive root C_*^+.

The value of H_*^+ can be then obtained from (9). For the nonnegativity of the latter we must impose

$$C_*^+ \geq \frac{1}{fr_H}(m_H + kL_2). \tag{10}$$

Explicitly, this simplifies to

$$\sqrt{[r_H(m_H + kL_2) - nz]^2 + 4fr_H^2 egzL_2P_2} + r_H(m_H + kL_2) - nz \geq 2r_H(m_H + kL_2) \geq 0$$

It can be rewritten as

$$\sqrt{[r_H(m_H + kL_2) - nz]^2 + 4fr_H^2 egzL_2P_2} \geq nz + r_H(m_H + kL_2) > 0\,,$$

from which, squaring and simplifying we get

$$fr_H egL_2P_2 \geq n(m_H + kL_2). \tag{11}$$

Explicitly, using (7) the above equation gives

$$\begin{aligned} fr_H eg[r_L(r_P - m_P) - bm_L][gm_L + a(r_P - m_P)] \\ \geq n(gr_L + ab)\{m_H(gr_L + ab) + k[r_L(r_P - m_P) - bm_L]\}. \end{aligned} \tag{12}$$

Let $Z = r_P - m_P$. From (12) we obtain the quadratic inequality in Z

$$A_2Z^2 + A_1Z + A_0 \geq 0, \tag{13}$$

where

$$\begin{aligned} &A_0 = -bfr_H eg^2m_L^2 - nm_H\delta^2 + nk\delta bm_L, \\ &A_1 = (gr_L - ab)m_L fr_H eg - knr_L, \quad A_2 = afr_H egr_L > 0\,. \end{aligned}$$

The discriminant $\Delta = A_1^2 - 4A_0A_4$ of the associated with (13) equation is given explicitly by

$$\Delta = [(gr_L - ab)m_L fr_H eg - knr_L\delta]^2 + 4afr_H egr_L(bfr_H eg^2m_L^2 + nm_H\delta^2 - nk\delta bm_L)$$

so that the roots are

$$Z_\pm = \frac{1}{2afr_H egr_L}\left[knr_L\delta - (gr_L - ab)m_L fr_H eg \pm \sqrt{\Delta}\right]\,,$$

or

$$Z_{\pm} = \frac{1}{2afr_Hegr_L}\Bigg[knr_L\delta - (gr_L - ab)m_Lfr_Heg$$
$$\pm\sqrt{[(gr_L - ab)m_Lfr_Heg - knr_L\delta]^2 + 4afr_Hegr_L(bfr_Heg^2m_L^2 + nm_H\delta^2 - nk\delta bm_L)}\Bigg].$$

For $A_0 < 0$ i.e.

$$nk\delta bm_L \le bfr_Heg^2m_L^2 + nm_H\delta^2 \tag{14}$$

the smaller root $Z_- < 0$, and we need

$$r_P \ge m_P + Z_+. \tag{15}$$

Conversely, for

$$nk\delta bm_L \ge bfr_Heg^2m_L^2 + nm_H\delta^2 \tag{16}$$

ir follows $Z_- > 0$ and we need

$$r_P \le m_P + Z_-, \quad r_P \ge m_P + Z_+. \tag{17}$$

In summary, coexistence is feasible whenever the condition (8) holds either coupled with (14) and (15), or coupled with (16), (17).

3.3 Stability

The Jacobian of (1) is

$$\mathbf{J} = \begin{bmatrix} J_{11} & r_LL & 0 & 0 \\ -gP & J_{22} & 0 & 0 \\ egP & egL & -r_HH - n & -r_HC \\ -kH & 0 & fr_HH & fr_HC - m_H - kL - 2zH \end{bmatrix}$$

with

$$J_{11} = r_LP - m_L - 2aL, \quad J_{22} = -gL + r_P - m_P - 2bP.$$

At the point E_0 the Jacobian $\mathbf{J}$ becomes a diagonal matrix, with entries $-m_L < 0$, $r_P - m_P$, $-n < 0$, $-m_H < 0$, so that E_0 is locally stable if

$$r_P < m_P. \tag{18}$$

i.e. if the opposite of the feasibility condition for E_1 (2), holds.

At E_1 the Jacobian is a lower triangular matrix, again with the explicit eigenvalues $r_LP_1 - m_L$, $r_P - m_P - 2bP_1$, $-n < 0$, $-m_H < 0$, which, in view of the feasibility condition (2), give the stability condition

$$0 < r_P - m_P < \frac{m_Lb}{r_L}. \tag{19}$$

Table 2 Equilibria, their feasibility and stability conditions

Equilibrium	Feasibility	Stability
$E_0 = (0,0,0,0)$	–	$r_P < m_P$
$E_1 = (0, P_1, 0, 0)$	$r_P \geq m_P$	$0 < r_P - m_P < b\frac{m_L}{r_L}$
$E_2 = (L_2, P_2, C_2, 0)$	$r_P - m_P \geq \frac{bm_L}{r_L} \geq 0$	$fr_H C_2 < m_H + kL_2$
$E_* = (L_*, P_*, C_*, H_*)$	$fr_H C_2 \geq m_H + kL_2$ and either (14), (15) or (16), (17)	– –

From now on, let $\mathbf{J}^{(i,k)}$ denote the block of $\mathbf{J}$ made of the i and k rows and columns, $i, k = 1, \ldots, 4$.

The characteristic equation at E_2 factorizes into the product of two quadratic equations. The block $\mathbf{J}^{(3,4)}$ is an upper triangular matrix, with eigenvalues $-n < 0$ and $fr_H C_2 - m_H - kL_2$. Applying the Routh-Hurwitz conditions to the block $\mathbf{J}^{(1,2)}$ we obtain

$$-\mathrm{tr}\left(\mathbf{J}^{(1,2)}(E_2)\right) = aL_2 + bP_2 > 0, \quad \det\left(\mathbf{J}^{(1,2)}(E_2)\right) = abL_2P_2 + gr_L L_2 P_2 > 0,$$

therefore not contributing to the stability. Hence E_2 is stable for

$$fr_H C_2 < m_H + kL_2. \tag{20}$$

This is the opposite of (10), namely the feasibility condition for E_*.

The characteristic equation at E_* factorizes into the product of two quadratic equations. Applying the Routh-Hurwitz conditions to each one of 2×2-blocks on the main diagonal of $\mathbf{J}$, i.e. $\mathbf{J}^{(1,2)}$ and $\mathbf{J}^{(3,4)}$ at each equilibrium we respectively obtain

$$-\mathrm{tr}\left(\mathbf{J}^{(1,2)}(E_*)\right) = aL_* + bP_* > 0, \quad \det\left(\mathbf{J}^{(1,2)}(E_*)\right) = abL_*P_* + gr_L L_* P_* > 0,$$

stability conditions that are therefore satisfied. For the lower block $\mathbf{J}^{(3,4)}$ we have

$$-\mathrm{tr}\left(\mathbf{J}^{(3,4)}(E_*)\right) = eg\frac{L_*P_*}{C_*} + zH_* > 0, \quad \det\left(\mathbf{J}^{(3,4)}(E_*)\right) = egz\frac{H_*}{C_*}[L_*P_* + fr_H^2 C_*^2] > 0,$$

once again satisfied. Hence, if feasible, E_* is unconditionally stable. Note also that there are no parameter combinations for which both traces vanish, thereby preventing the onset of Hopf bifurcations at this point.

4 Bifurcations

Using Sotomayor's theorem, [19], we can establish the transcritical bifurcations that are suggested to exist between the pairs of equilibria $E_0 - E_1$, $E_1 - E_2$ and $E_2 - E_*$ by the corresponding feasibility and stability conditions, see Table 2. We denote by F the right-hand side of (1).

4.1 Bifurcations from the extinction state E_0

Taking as bifurcation parameter $n_P = r_P - m_P$, we find that for the threshold value $n_P^\dagger = 0$, one eigenvalue of the Jacobian of (1) at the extinction state E_0 vanishes. The right and left eigenvectors of the Jacobian evaluated at this point are $v = w = (0, 1, 0, 0)^T$.

On the one hand, we find

$$\partial_{n_P} F|_{E_0} = \left.(0, P, 0, 0)^T\right|_{E_0} = (0, 0, 0, 0)^T\,,$$

so that

$$w^T \partial_{n_P} F\Big|_{E_0} = 0,$$

which prevents a saddle-node bifurcation to occur.

On the other hand,

$$\mathbf{D}\partial_{n_P} F|_{E_0} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

and thus

$$w^T \mathbf{D}\ \partial_{n_P} F|_{E_0} v = 1 \neq 0.$$

Also,

$$w^T \mathbf{D}^2 F(v, v) = -2b \neq 0$$

and Sotomayor's theorem implies the existence of a transcritical bifurcation with E_1 at $n_P = 0$.

4.2 Bifurcation from prey-only state E_1

Considering now E_1, for the threshold value $n_P^\ddagger = b m_L r_L^{-1}$ again one eigenvalue of the Jacobian evaluated at this point vanishes. The left and right eigenvalues of $\mathbf{J}$ are $w = (1, 0, 0, 0)^T$ and $v = (v_1, v_2, v_3, 0)^T$, with

$$v_1 = -b, \quad v_2 = g, \quad v_3 = -\frac{eg}{n} n_P.$$

Here

$$\partial_{n_P} P|_{E_1} = \left.(0, P, 0, 0)^T\right|_{E_1} = (0, P_1, 0, 0)^T = \left(0, \frac{n_P}{b}, 0, 0\right)^T$$

so that

$$w^T \partial_{n_P} F\Big|_{E_1} = 0,$$

which again prevents the occurrence of a saddle-node bifurcation. Further,

$$\mathbf{D}\partial_{n_P}F|_{E_1} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

and thus

$$w^T\mathbf{D}\;\partial_{n_P}F|_{E_1}\,v = 0.$$

Therefore, Sotomayor's theorem is inconclusive in this case.

Taking instead as bifurcation parameter r_L, with threshold value $r_L^\dagger = bm_L(r_P - m_P)^{-1}$, we find the same pair of eigenvectors as above, $w = (1,0,0,0)^T$ and $v = (v_1, v_2, v_3, 0)^T$. Further,

$$\partial_{r_L}F = (LP, 0, 0, 0)^T, \quad \text{so} \quad \partial_{r_L}F|_{E_1} = (0,0,0,0)^T.$$

which implies

$$w^T\partial_{r_L}F\big|_{E_1} = 0,$$

and

$$\mathbf{D}\partial_{r_L}F|_{E_1} = \left.\begin{bmatrix} P & L & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}\right|_{E_1} = \begin{bmatrix} P_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}.$$

It follows

$$w^T\mathbf{D}\partial_{n_P}F|_{E_1}v = P_1v_1 \neq 0.$$

We need also to evaluate

$$w^T\mathbf{D}^2F(v,v) = \mathbf{D}^2F_1(v,v) = 2r_Lv_1v_2 - 2av_1^2 = 2v_1(r_Lv_2 - av_1) = -2b(r_Lg + ab) \neq 0$$

and Sotomayor's theorem implies that a transcritical bifurcation with E_2 exists at $r_L = r_L^\dagger$.

4.3 Bifurcation from hyena-free state E_2

Take as bifurcation parameter r_H with $r_H^\dagger = (m_H + kL_2)(fC_2)^{-1}$. Here

$$\mathbf{J}(E_2, r_H^\dagger) = \begin{bmatrix} -aL_2 & r_LL_2 & 0 & 0 \\ -gP_2 & -bP_2 & 0 & 0 \\ egP_2 & egL_2 & -n & -r_HC_2 \\ 0 & 0 & 0 & fr_HC_2 - kL_2 - m_H \end{bmatrix},$$

where the last row vanishes for $r_H = r_H^\dagger$. Hence the eigenvectors are $w^T = (0,0,0,1)$, $v^T = (0,0,r_HC_2,-n)$.

We have

$$\partial_{r_H}F = (0,0,CH,fCH)^T, \quad \partial_{r_H}F|_{E_2} = (0,0,0,0)^T.$$

so that

$$w^T \partial_{r_H} F\big|_{E_2} = 0,$$

Next

$$\mathbf{D}\partial_{r_H} F|_{E_2} = \left.\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & H & C \\ 0 & 0 & fH & fC \end{bmatrix}\right|_{E_2} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & C_2 \\ 0 & 0 & 0 & fC_2 \end{bmatrix}$$

It follows

$$w^T \, \partial_{r_H} F|_{E_2} = 0.$$

Moreover,

$$w^T \, \mathbf{D}\partial_{r_H} F|_{E_2} \, v = -nfC_2 \neq 0.$$

Also,

$$w^T \mathbf{D}^2 F(v,v) = \mathbf{D}^2 F_4(v,v) = 2fr_H v_3 v_4 - 2zv_4^2 = -2n(fr_H^2 C_2 + nz) \neq 0.$$

These results indicate the onset of a transcritical bifurcation with E_*.

4.4 Simulations

In all simulations the initial conditions are

$$L(0) = 0.9, \quad P(0) = 0.7, \quad C(0) = 0.0, \quad H(0) = 0.7. \tag{21}$$

Purely hypothetical reference parameter values, that give E_0, see left frame of Figure 1, are:

$$\begin{gathered} r_L = 2.5, \quad m_L = 0.5, \quad a = 0.8, \quad g = 0.2, \quad r_P = 0.4, \quad m_P = 0.8, \quad b = 3.0, \\ e = 0.1, \quad r_H = 0.02, \quad n = 0.09, \quad f = 0.1, \quad m_H = 0.03, \quad k = 0.1, \quad z = 0.6. \end{gathered} \tag{22}$$

In Figure 1, right frame, instead, E_1 is obtained by taking in place of the values of (22) the following ones

$$r_P = 1.2, \quad m_P = 0.8. \tag{23}$$

For E_2 the different choices than (22) are

$$r_P = 3.4, \quad m_P = 0.1. \tag{24}$$

and the plot appears in the left frame of Figure 2, while for E_* the changes are

$$g = 1.8, \quad r_P = 3.4, \quad m_P = 0.1, \quad e = 0.9, \quad r_H = 18, \quad n = 0.01, \quad f = 0.5. \tag{25}$$

We also provide bifurcation diagrams. Figure 3 is obtained with the parameters (22) with the exception of the bifurcation parameter ranging in

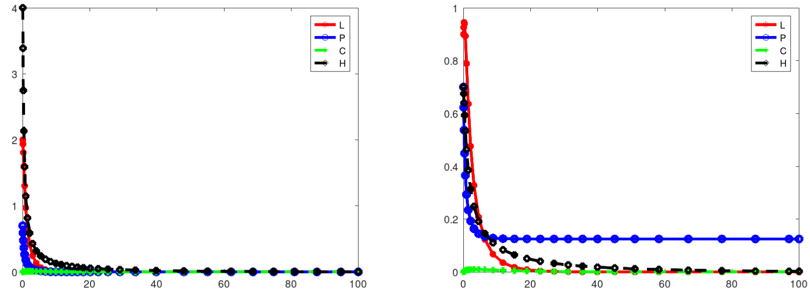

Fig. 1 Left: Equilibrium E_0 is attained with the parameter values (22). Right: Equilibrium E_1 is obtained with (22) in which the parameters (23) are replaced.

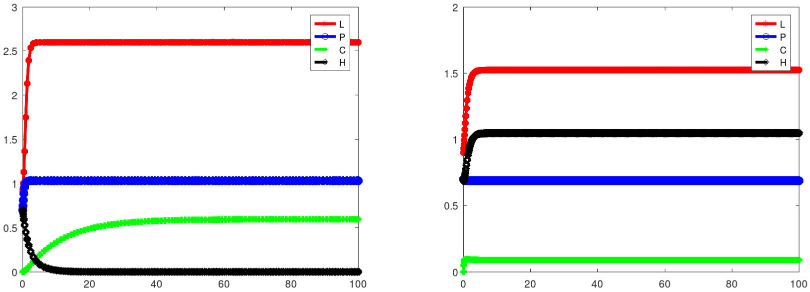

Fig. 2 Left: Equilibrium E_2 is obtained with (22) with the replacement (24). Right: To obtain E_* the parameters of (25) are used, while the remaining ones come from (22).

$r_P \in [0, 2]$. For increasing values of the latter, E_0 shows a transcritical bifurcation at $r_P^\dagger = 0.8$ leading to equilibrium E_1, in agreement with the theoretical results, here indeed $r^\dagger = m_P = 0.8$. At $r_P^\ddagger = 1.4$ a new transcritical bifurcation from which E_2 arises is observed. Again this fits the theoretical analysis, as $r^\ddagger = m_P + bm_L r_L^{-1} = 1.4$.

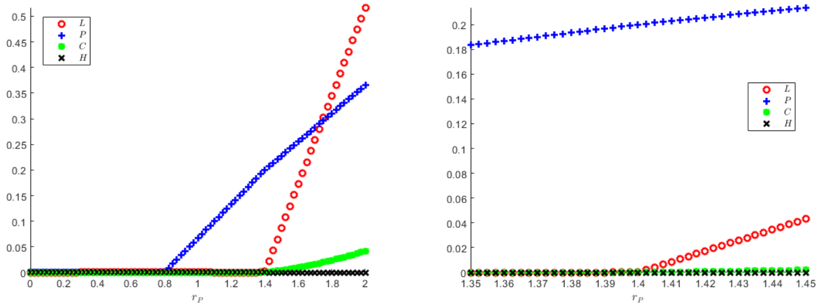

Fig. 3 Left: Bifurcation diagram as function of r_P, with the parameters (22). Right: a blow up of the left frame near the threshold value $r^\ddagger$.

In Figure 4 the parameters are once again those of (22), in which however the modification (25) is taken into account, where once again the bifurcation parameter is $r_P \in [0, 2]$. Again a chain of transcritical bifurcations is observed, at first taking E_0 into E_1 for $\widetilde{r}_P = 0.1$ and then from E_1 to E_* for $\widehat{r}_P = 0.7$. Again, the first result is in agreement with Table 2. Indeed in this case $\widetilde{r}_P = m_P = 0.1$ while for the other one we know that Sotomayor's theorem is inconclusive, and we have only the numerical result.

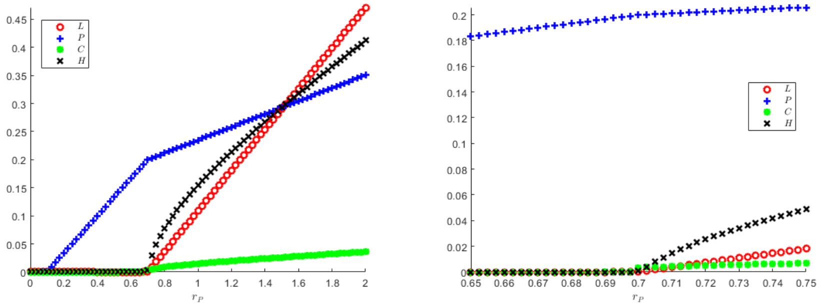

Fig. 4 Parameters given in (22), with the change of (25). Left: Bifurcation diagram as function of r_P. Right: a blow up of the left frame near the threshold value $\widehat{r}_P$.

Thus E_1 not necessarily bifurcates only into E_2 when $r_P > m_P + \frac{bm_L}{r_L}$. The simulation indicates that when r_P falls below the threshold $\widehat{r}_P$, coexistence E_* shows a transcritical bifurcation directly with E_1.

5 Model with hyenas interference

We introduce a feedback from the hyena population (scavenger) to the lion population (predator) by modifying the reproduction rate r_L, which now depends on the density of hyenas and takes the form: $\frac{r_L}{1+\alpha H}$. This formulation is motivated by the cost imposed by the hyenas onto the lions. Hyenas acquire carcasses from lions before the lions are able to consume much of the carcasses, by hyenas mobbing, or by hyenas killing the lions' cubs [13, 14, 16]. This has an indirect effect on the lions' reproduction rate introduced by interspecific interference, which reduces the amount of resource available to the lions - be it due to killing of lion cubs, kleptoparasitism, or distraction from prey and its subsequent loss to other predators, such as vultures.

The parameter α is assumed to be positive, but small not just since hyena kleptoparasitism is more efficient in the absence of male lions [14, 15], but also because of local-scale avoidance strategy between the two carnivore populations [18]. In fact, field observations report that hyaenas never access a lion kill in the presence of male lions, whereas if only lionesses and cubs are present at the killing site, hyenas remain in the vicinity and even drive the lions away [14].

The equations of the extension to model (1) thus read

$$\frac{dL}{dt} = \frac{r_L}{1+\alpha H} LP - m_L L - aL^2 \tag{26a}$$

$$\frac{dP}{dt} = -gLP + r_P P - m_P P - bP^2 \tag{26b}$$

$$\frac{dC}{dt} = egLP - r_H CH - nC \tag{26c}$$

$$\frac{dH}{dt} = fr_H CH - m_H H - kHL - zH^2. \tag{26d}$$

The scenario modelled in (26) represents the scheme of interactions between lions and hyenas depicted in [13, Fig. 2]. Lions affect hyenas in two ways: negatively through killing, but positively by providing scavenging and kleptoparasitism opportunities. The hyenas' effect on lions is less pronounced and captured by the small value of α.

The boundedness of the solutions can be demonstrated as in Section 3.1. Some of the nontrivial equilibria of (1) carry over to this model, namely, the prey-only state E_1, the hyena-free state E_2. The coexistence state E_* requires the solution of a highly nonlinear system, which is not solvable analytically.

The Jacobian of the right-hand side of (26) takes

$$\mathbf{J} = \begin{pmatrix} \frac{r_L P}{1+\alpha H} - 2aL - m_L & \frac{r_L L}{1+\alpha H} & 0 & -\frac{\alpha r_L LP}{(1+\alpha H)^2} \\ -gP & n_P - 2bP - gL & 0 & 0 \\ egP & egL & -n - r_H H & -r_H C \\ -Hk & 0 & fr_H H & fr_H C - kL - 2zH - m_H \end{pmatrix}.$$

We study now the bifurcation structure of the model (26). We denote by $\tilde{F}$ the right-hand side of (26).

5.1 Bifurcation from prey-only state E_1

We use as bifurcation parameter r_L with threshold value $r_L^\dagger = \frac{bm_L}{n_P}$. The Jacobian of the right-hand side of (26) evaluated at $E_1 = (0, \frac{n_P}{b}, 0, 0)$ is given by

$$\mathbf{J}(E_1, r_L^\dagger) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ -\frac{gn_P}{b} & -n_P & 0 & 0 \\ \frac{egn_P}{b} & 0 & -n & 0 \\ 0 & 0 & 0 & -m_H \end{pmatrix}.$$

Its left and right eigenvectors w, v are explicitly given:

$$w = (1,0,0,0)^T, \quad v = \left(\frac{bn}{egn_P}, -\frac{n}{en_P}, 1, 0\right)^T.$$

We have

$$\partial_{r_L}\tilde{F} = \left(\frac{LP}{1+\alpha H}, 0, 0, 0\right)^T, \quad \text{so} \quad \partial_{r_L}\tilde{F}|_{E_1} = (0,0,0,0)^T$$

which imposes

$$w^T \partial_{r_L}\tilde{F}\Big|_{E_1} = 0,$$

preventing a saddle-node bifurcation from E_1 at $r_L^{\dagger}$. Next,

$$\mathbf{D}\partial_{r_L}\tilde{F}\Big|_{E_1} = \left.\begin{bmatrix} \frac{P}{1+\alpha H} & \frac{L}{1+\alpha H} & 0 & -\frac{\alpha LP}{(1+\alpha H)^2} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}\right|_{E_1} = \begin{bmatrix} P_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}.$$

This gives

$$w^T\mathbf{D}\ \partial_{r_L}\tilde{F}\Big|_{E_1} v = \frac{bn}{egn_P} \neq 0,$$

and

$$w^T\mathbf{D}^2\tilde{F}(v,v) = -\frac{2ab^2n^2}{e^2g^2n_P^2} - \frac{2b^2m_Ln^2}{e^2gn_P^3} \neq 0$$

Sotomayor's theorem shows that a transcritical bifurcation with E_2 exists at the value $r_L = r_L^{\dagger}$.

5.2 Bifurcation from hyena-free state E_2

We use as bifurcation parameter r_L, with $r_L^{\dagger}$ such that $r_H = \frac{m_H+kL_2}{fC_2}$. The solutions for r_L are given by the quadratic

$$\begin{aligned}\Pi(r_L) = gn(m_Hg+kn_P)r_L^2+(bng(am_H-km_L)+abn(gm_H+kn_P)-efgn_Pr_H(an_P+gm_L) \\ + ab^2n(am_H-km_L)+befgm_Lr_H(an_P+gm_L) = 0\,, \quad (27)\end{aligned}$$

which has as solutions

$$r_L^{\dagger} = \frac{\pm(an_P+gm_L)\Delta^{1/2} - (2agm_H+akn_P-gkm_L)bn + (an_P+gm_L)efgn_Pr_H}{2n(m_Hg^2+kn_Pg)},$$

where

$$\Delta = (bkn - efgn_Pr_H)^2 - 4m_Hbefg^2nr_H.$$

Note that we cannot have just one positive root $r_L^{\dagger}$ to this quadratic (27). In fact, let us argue by reduction to absurdity. The conditions for only one positive root $r_L > 0$ is $\Pi(0) < 0$ or

$$k > a\frac{m_H}{m_L} + \frac{efgr_H}{abn}(an_P + gm_L)$$

Since the leading term of (27) is positive, in order for the feasibility condition (8) to hold, we must have $r_L^\dagger > \frac{bm_L}{n_P}$ and $\Pi(\frac{bm_L}{n_P}) < 0$. However, $\Pi(\frac{bm_L}{n_P}) = m_H$, which is a contradiction.

So long as the roots to (27) $r_L^\dagger$ are real, we have the Jacobian

$$\mathbf{J}(E_2, r_L^\dagger) = \begin{pmatrix} -aL_2 & r_L^\dagger L_2 & 0 & -\alpha r_L^\dagger L_2 P_2 \\ -gP_2 & -bP_2 & 0 & 0 \\ egP_2 & egL_2 & -n & -r_H C_2 \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

and

$$\partial_{r_L}\tilde{F} = (\frac{LP}{1+\alpha H}, 0, 0, 0)^T, \quad \partial_{r_L}\tilde{F}|_{E_2} = (L_2P_2, 0, 0, 0)^T.$$

The left eigenvector of $\mathbf{J}$ is $w = (0,0,0,1)^T$, implying that

$$w^T \partial_{r_L}\tilde{F}|_{E_2} = 0.$$

However,

$$\mathbf{D}\partial_{r_L}\tilde{F}\Big|_{E_2} = \left.\begin{bmatrix} \frac{P}{1+\alpha H} & \frac{L}{1+\alpha H} & 0 & \frac{-\alpha LP}{(1+\alpha H)^2} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}\right|_{E_2} = \begin{bmatrix} P_2 & L_2 & 0 = \alpha L_2 P_2 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

which satisfies $w^T\ \mathbf{D}\partial_{r_L}\tilde{F}\Big|_{E_2} v = 0$ for any v. Therefore, Sotomayor's theorem is inconclusive in this case. A numerical example will illustrate what happens for these values of $r_L^\dagger$.

Alternatively we use as bifurcation parameter r_H, with $r_H^\dagger = \frac{m_H + kL_2}{fC_2}$. The Jacobian at this point is

$$\mathbf{J}(E_2, r_H^\dagger) = \begin{pmatrix} -aL_2 & r_L L_2 & 0 & -\alpha r_L L_2 P_2 \\ -gP_2 & -bP_2 & 0 & 0 \\ egP_2 & egL_2 & -n & -r_H C_2 \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

with L_2, P_2 given by (7). Its left and right eigenvectors w, v are explicitly given: $w = (0,0,0,1)^T$ and $v = (v_1, v_2, v_3, 1)^T$, where

$$v_1 = -\frac{a\alpha b n_P r_L + \alpha b g m_L r_L}{\delta^2},$$

$$v_2 = \frac{\alpha m_L r_L g^2 + a\alpha n_P r_L g}{\delta^2},$$

$$v_3 = -\frac{1}{fn\delta^3}\Big(m_H a^3 b^3 - ka^2b^3m_L + a^2b^2r_L(3m_Hg + kn_P) + \alpha efa^2bgn_P^2r_L - 2kab^2gm_Lr_L$$

$$+ abr_Lg(3\alpha efgm_Ln_P + 3m_Hgr_L + 2kn_Pr_L) - \alpha efag^2n_P^2r_L^2 + 2\alpha efbg^3m_L^2r_L$$
$$\left. - kbg^2m_Lr_L^2 - \alpha efg^3m_Ln_Pr_L^2 + m_Hg^3r_L^3 + kg^2n_Pr_L^3\right) .$$

We have

$$\partial_{r_H}\tilde{F} = (0,0,-CH,fCH)^T, \quad \partial_{r_H}\tilde{F}|_{E_2} = (0,0,0,0)^T.$$

so that

$$w^T\partial_{r_H}\tilde{F}|_{E_2} = 0.$$

Next

$$\mathbf{D}\partial_{r_H}\tilde{F}\Big|_{E_2} = \left.\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -H & -C \\ 0 & 0 & fH & fC \end{bmatrix}\right|_{E_2} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -C_2 \\ 0 & 0 & 0 & fC_2 \end{bmatrix}$$

It follows

$$w^T\mathbf{D}\partial_{r_H}\tilde{F}|_{E_2}v = -\frac{efg(an_P + gm_L)(bm_L - n_Pr_L)}{n(ab + gr_L)^2} \neq 0.$$

Also,

$$w^T\mathbf{D}^2\tilde{F}(v,v) = \frac{k(a\alpha bn_Pr_L + \alpha bgm_Lr_L)}{(ab + gr_L)^2}$$
$$+ (m_H - \frac{k(bm_L - n_Pr_L)}{ab + gr_L}) \times \frac{f-1}{ef^2g(ab + gr_L)(an_P + gm_L)(bm_L - n_Pr_L)}$$
$$\times (m_H(ab + gr_L)^3 + ka^2b^2(n_Pr_L - bm_L) + \alpha efa^2bgn_P^2r_L$$
$$+ 3\alpha efabg^2m_Ln_Pr_L + 2kabgr_L(n_Pr_L - bm_L) - \alpha efag^2n_P^2r_L^2$$
$$+ 2\alpha efbg^3m_L^2r_L - \alpha efg^3m_Ln_Pr_L^2 + kg^2r_L^2(n_Pr_L - bm_L)) > 0.$$

when $\alpha \approx 0$.

In principle, there may exist $\alpha > 0$ such that $w^T\mathbf{D}^2\tilde{F}(v,v) = 0$. However, since the fourth component of $\tilde{F}$ contains at most quadratic nonlinearities, $w^T\mathbf{D}^3\tilde{F}(v,v,v) \equiv 0$, so Sotomayor's theorem prevents the onset of a pitchfork bifurcation from E_2 at $r_H^\dagger$.

These results indicate the onset of a transcritical bifurcation with a coexistence equilibrium E_*.

5.3 Simulation

We set as parameters

$$m_L = 0.05;\ r_P = 2.4;\ m_P = 0.1;\ m_H = 0.03;\ k = 0.5;\ e = 0.57;\ g = 2.8;$$
$$\alpha = 0.005;\ f = 2.25;\ a = 1;\ b = 5;\ n = .2;\ z = 1;\ r_H = 0.8 \quad (28)$$

and study the bifurcation of (26) as r_L varies in the interval $[0, 30]$.

The hyena-free state E_2 bifurcates at $r_L = 0.1087$ from the prey-only state $E_1 = (0, 0.46, 0, 0)$ via a transcritical bifurcation as the analysis shows. This state becomes, however, locally asymptotically unstable for values $r_L \in (0.11998, 21.7551)$ (dashed line in Figure 5) and becomes stable again for $r_L > 21.7551$ (solid line in Figure 5). At $r_L = 0.11998$ the coexistence point E_* branches from E_2 in a transcritical bifurcation and once again at $r_L = 21.7551$ as a subcritical bifurcation (solid line in Figure 5).

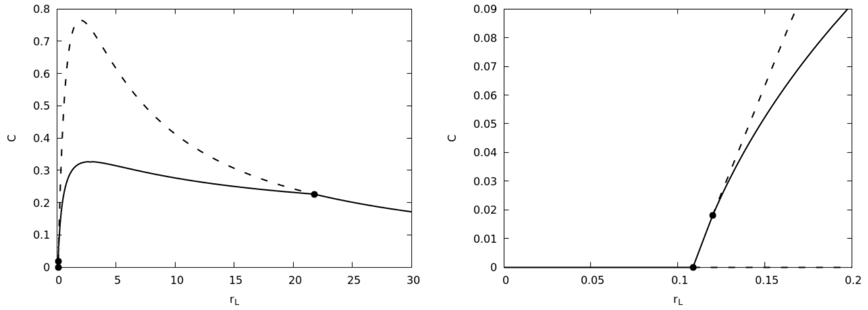

Fig. 5 Bifurcation diagrams as function of r_L (on the right a blow up in the range $[0, 0.2]$). The transcritical bifurcation is denoted by $\bullet$. Parameters given in (28).

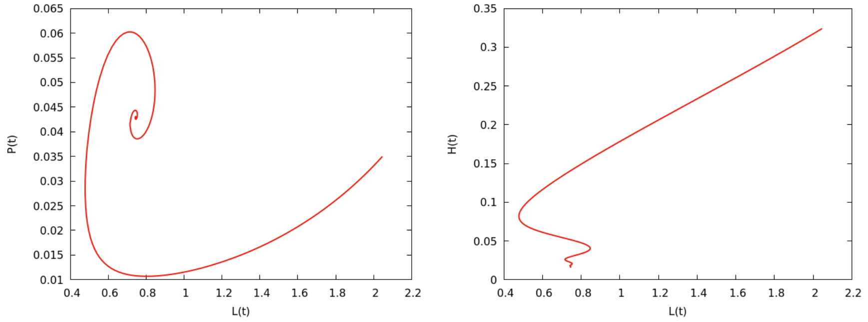

Fig. 6 The coexistence equilibrium E_* for model (26) is a stable spiral. Parameters given in (28) with $r_L = 18.5$ and initial values $L(0) = 2.0458, P(0) = 0.035, C(0) = 0.001, H(0 = 0.3241$.

Figure 6 illustrates the trajectory of model (26) for the stable coexistence equilibrium. Unlike the model without feedback (1), here we observe damped oscillations to the equilibirum.

5.4 Simplified case

For simplicity of the analysis, we discount the interspecific competition for the lions, prey and hyenas, and work with the system

$$\frac{dL}{dt} = \frac{r_L}{1+\alpha H} LP - m_L L \tag{29a}$$

$$\frac{dP}{dt} = -gLP + r_P P - m_P P \tag{29b}$$

$$\frac{dC}{dt} = egLP - r_H CH - nC \tag{29c}$$

$$\frac{dH}{dt} = fr_H CH - m_H H - kHL. \tag{29d}$$

Observe that (29) does not permit a prey-only state unless $r_P = m_P$.

The values at the hyena-free state E_2 can be computed explicitly

$$L_2 = \frac{n_P}{g}, P_2 = \frac{m_L}{r_L}, C_2 = \frac{em_L n_P}{nr_L}, H_2 = 0.$$

The values at the coexistence state E_* can also be computed explicitly:

$$L_* = \frac{n_P}{g}, \quad C_* = \frac{m_H + kL^*}{fr_H}, \quad H_* = \frac{egm_L L_* - nr_L C_*}{r_H r_L C_* - \alpha egm_L L_*}, \quad P_* = \frac{m_L}{r_L}(1+\alpha H_*),$$

which is feasible if

$$(efgm_L n_P r_H - nr_L(gm_H + kn_P))(r_L(gm_H + kn_P) - \alpha fgm_L n_P) \geq 0$$
$$\text{and} \quad r_L(gm_H + kn_P) \neq \alpha fgm_L n_P. \tag{30}$$

The Jacobian matrix of the system (29) is:

$$\mathbf{J}(L,P,C,H) = \begin{pmatrix} \frac{r_L}{1+\alpha H}P - m_L & \frac{r_L}{1+\alpha H}L & 0 & \frac{-\alpha r_L LP}{(1+\alpha H)^2} \\ -gP & -gL + r_P - m_P & 0 & 0 \\ egP & egL & -r_H H - n & -r_H C \\ -kH & 0 & fr_H H & fr_H C - m_H - kL \end{pmatrix}$$

At the extinction equilibrium E_0 the Jacobian has eigenvalues $-m_L, -n, r_P - m_P, -m_H$, so this point is unstable in view of condition (2).

At the hyena-free state E_2,

$$\mathbf{J}(E_2) = \begin{pmatrix} 0 & r_L L_2 & 0 & -\alpha r_L L_2 P_2 \\ -gP_2 & 0 & 0 & 0 \\ egP_2 & egL_2 & -n & -r_H C_2 \\ 0 & 0 & 0 & fr_H C_2 - m_H - kL_2 \end{pmatrix},$$

which has eigenvalues $-n, fr_HC_2 - m_H - kL_2, \pm i\sqrt{n_Pm_L}$. Hence, for the critical value of r_L or n_P such that $fr_HC_2 - m_H - kL_2 = 0$ we cannot apply Sotomayor's theorem, as two eigenvalues are purely imaginary. Hence, E_2 is a centre whenever $fr_HC_2 - m_H - kL_2 < 0$ and unstable fixed point whenever $fr_HC_2 - m_H - kL_2 = fr_H\frac{em_Ln_P}{nr_L} - \frac{gm_H+kn_P}{g} > 0$. The last condition is equivalent to the feasibility of E_*.

To conclude, model (29) has the following steady states summarised in Table 3.

Table 3 Equilibria of (29), their feasibility and stability conditions

Equilibrium	Feasibility	Stability
$E_0 = (0, 0, 0, 0)$	–	$r_P < m_P$
$E_2 = (L_2, P_2, C_2, 0)$	$r_P \geq m_P$	centre
$E_* = (L_*, P_*, C_*, H_*)$	(30)	–

Numerical simulations of (29) show that its behaviour resembles that of the classical Lotka-Volterra predator-prey model. The coexistence equilibrium for the lion-prey subsystem is always a neutral centre [20] leading to solutions that are periodic orbits, and are structurally unstable asymptotically. However, when the coexistence equilibrium exists, we consider a feedback coupling between the lion-prey subsystem and the carcass-hyena subsystem and show that the coexistence equilibrium loses this property.

The Jacobian matrix of the system (29) is:

$$\mathbf{J}(E_*) = \begin{pmatrix} 0 & \frac{r_L}{1+\alpha H_*}L_* & 0 & \frac{-\alpha r_L L_* P_*}{(1+\alpha H_*)^2} \\ -gP_* & 0 & 0 & 0 \\ egP_* & egL_* & -r_HH_* - n & -r_HC_* \\ -kH_* & 0 & fr_HH_* & 0 \end{pmatrix}$$

and gives the characteristic polynomial of fourth degree‘

$$\Pi(\lambda) = \pi_4\lambda^4 + \pi_3\lambda_3 + \pi_2\lambda_2 + \pi_1\lambda + \pi_0 = 0 \tag{31}$$

$$\pi_4 = gr_L(1 + H_*\alpha)$$
$$\pi_3 = (1 + \alpha H_*)gr_L(n + H_*r_H)$$
$$\pi_2 = (m_Ln_Pr_L(g + (g - k)H_*\alpha) + H_*(1 + \alpha H_*)kn_Pr_Hr_L + H_*(1 + H_*\alpha)gm_Hr_Hr_L)$$
$$\pi_1 = (H_*(g + (g - k)\alpha H_*)gm_Ln_Pr_Hr_L + (g + (g - k)H_*\alpha)m_Lnn_Pr_L + H_*\alpha(1 + H_*\alpha)ef$$
$$\pi_0 = m_Ln_Pr_H(1 + H_*\alpha)H_*((kn_P + gm_H)r_L - \alpha efgm_Ln_P)$$

where the coefficient are positive so long as $g > k$ and $(kn_P + gm_H)r_L - \alpha efgm_Ln_P > 0$, which is the feasibility condition for E_*.

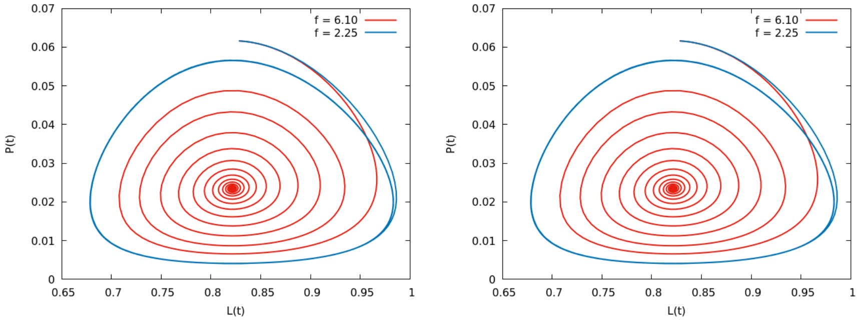

Fig. 7 The coexistence equilibrium E_* for the model with hyenas interference (29) is a neutral centre for $f = 2.25$ leading to a periodic orbit (blue) and a stable spiral for $f = 6.10$ (red).

The Routh-Hurwitz criteria for all roots of (31) to have negative real part are

$$\pi_i > 0, \quad \pi_2\pi_3 > \pi_1\pi_4, \quad \pi_1\pi_2\pi_3 > \pi_0\pi_3^2 + \pi_1^2\pi_4.$$

If $g > k$ (which means that we assume lions to have a higher killing rate for the prey than for hyenas), then all coefficients π_i of (31) are positive, and the third condition when true implies the second.

In other words, in the simplified model, as soon as the system can sustain the herbivores, the other species can invade it: first, the lions and then, the hyenas. In case of (26) indeed, the prey-only point is not an equilibrium, as it occurs instead in (1), because no other equilibrium where some population vanishes can exist.

A numerical simulation is provided in Figure 7. The initial conditions are $L(0) = 0.82798, P(0) = 0.06163, C(0) = 0.13426, H(0) = 0.10498$ and the parameter values used are

$$r_L = 2.5, \quad m_L = 0.05, \quad r_P = 2.4, \quad m_P = 0.1, \quad r_H = 0.8, \quad m_H = 0.03, \tag{32}$$
$$k = 0.5, \quad e = 0.58, \quad g = 2.8, \quad n = 0.2, \quad \alpha = 0.95.$$

6 Discussion and conclusion

We consider a model for the indirect interactions between two carnivore species: lions and hyenas. The mechanisms behind them are far from being understood [13], but their analysis through mathematical modelling is important for elucidating which factors are helpful or detrimental to their coexistence and eventual persistence in the African savanna ecosystem. In the proposed models we analyse an ecosystem of interacting consumer species: predators (lions) and scavengers (hyenas), which do not compete directly for resources, but participate in two linked trophic chains.

The model we consider is comprised of two subsystems, lions-prey and carcasses-hyenas. The first subsystem is a classical predator-prey system, where part of the prey resource serves as a consumer resource in the second subsystem. The two are loosely connected via the occasional killing of hyenas by lions, by the leftover prey carcasses after the lions hunting, and by hyenas interfering with lions at the prey killing site (kleptoparasitism).

In (1) the feedback from scavenger kleptoparasitism was neglected. Hence, the system has the dynamical structure of a trophic chain. This is also easily seen by the fact that the Jacobian is also a block triangular matrix. The dynamics of the carcass-hyenas subsystem is subjugate to that of the lions-prey subsystem. The bifurcation analysis shows that this model permits at most transcritical bifurcations, provided that the intraspecific competition rates are non-zero.

In (26) we consider the ecosystem with hyenas able to interfere with lions, thus having a negative effect on the lions' reproduction rate. This occurs either via reduced access to food at the lions' killing site where hyenas distract them from their prey (large groups of hyenas are capable of stealing the carcass even when lions are still present [13]) or by hyenas killing lion cubs. The model structure is that of a trophic chain where the consumers are subject to two-way competition due to their social and feeding behaviour as species. The bifurcation analysis shows that transcritical and subcritical bifurcations are possible between the hyenas-free state and the coexistence equilibrium. This is similar to the behaviour of the model without any feedback loops (1). However, the feedback loop introduces damped oscillations into the system, as shown in Fig. 6.

A simplified version of this model given in (29) shows that loose coupling of two trophic systems is sufficient to rectify the well-known shortcoming of the Lotka-Volterra system, namely, the neutral centre property of the coexistence equilibrium between prey and predator. Its analysis shows that as soon as the ecosystem can sustain the herbivores, the carnivore species can invade it: first, the lions and then, the hyenas. This prediction agrees with field data that hyena and lion densities across sites in Africa are positively correlated. This fact suggests that coexistence between lions and hyenas is ensured primarily by prey abundance and not by the one of the carnivore competitor [13].

Similar models for coupled consumer-resource subsystems have been considered also elsewhere in the literature. For instance, [21] is a study a predator-prey system where the predator can feed on a supplementary resource. The authors in [22] consider a predator-prey system where leftovers (carcasses) serve as a secondary resource for scavengers. They consider however, a Rosenzweig-MacArthur-type interaction for the predator and prey, which produces an oscillatory regime with a limit cycle. The model in [23] presents a case where scavengers (wild boars) and prey (deer) compete for grazing, but the scavengers feed as well on the prey's carcasses. However, the two scenarios considered by us are based on the assumptions that carnivores very rarely eat other carnivores. This discounts the opportunity for the scavengers to consume additional resources unlike the situation modelled in [23] since wild boars are omnivores. Other authors consider scenario for competition between two predator species with different preferences between prey and carcasses [24].

In this work, we study how the predator is affected by the scavengers interfering with it indirectly, not via mutual effects on the handling times. Unlike our model, both studies [23, 24] introduce the competition relation between the predators via the functional form of predation. The analysis of the scenarios with and without negative feedback loop onto the lions' reproduction rate shows that the dynamical behaviour of the system is not significantly affected, except that damped oscillations to the stable coexistence equilibrium are possible when taking into account the hyenas' interference onto the lions.

Like all models, the ones proposed here are simplifications of reality. As such, they have their own limitations, that we now proceed to describe. Our models do not take into account kleptoparasitism of lions onto hyenas, nor hyenas preying onto smaller herbivores. Field observations suggest that these could also be important factors in maintaining the coexistence between the carnivore competitors [13]. We have also neglected spatio-temporal relationships between hyenas and lions. This assumption is rooted in the fact that their hunting habitats do not fully overlap, and lions unlike hyenas generally need vegetation cover to ambush prey. Finally, the models could be extended using spatially-distributed variables for the populations.

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Declarations

- Competing interests: The authors declare no competing interests directly or indirectly related to the work submitted for publication.
- Conflict-of-interest statement: The authors have no conflicts of interest to declare.

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