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On the (dis) advantages of cannibalism

Abstract. Cannibalism is an interaction between individuals that can produce counter-intuitive effects at the population level. A striking effect is that a population may persist under food conditions such that the non-cannibalistic variant is doomed to go extinct. This so-called life boat mechanism has received considerable attention. Implicitly, such studies sometimes suggest, that the life boat mechanism procures an evolutionary advantage to the cannibalistic trait.

Here we compare, in the context of a size structured population model, the conditions under which the life boat mechanism works, with those that guarantee, that a cannibalistic mutant can invade successfully under the steady environmental conditions as set by a non-cannibalistic resident. We find qualitative agreement and quantitative difference. In particular, we find that a prerequisite for the life boat mechanism is, that cannibalistic mutants are successful invaders. Roughly speaking, our results show that cannibalism brings advantages to both the individuals and the population when adult food is limiting.

1. Introduction

Cannibalism is an intriguing phenomenon as it seems, almost literally, like cutting into ones own flesh. The aim of this paper is, to contribute to the weighing of advantages against disadvantages, with due attention for the distinction between the individual level and the population level.

To set the scene, we first give an incomplete list of relevant aspects, while referring to the survey article (Polis 1981) and to our concluding section for a more complete and detailed list and especially to (Polis 1981) for numerous references.

By practicing cannibalism, an individual gains energy (perhaps in the precious form of a scarce resource, like protein). Moreover, it eliminates a (potential, future) rival (for mates), competitor (for food) and aggressor (of offspring).

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As emphasized by BSE among cattle and Kuru among humans, (involuntary) cannibalism may strongly contribute to pathogen transmission. Moreover, it may lead to injuries (in particular, when the size difference between agressor and potential victim is not too big).

In this paper we ignore pathogens. Moreover, we take size differences between individuals into account and assume, that the size of the potential victim is so much smaller than that of the cannibal, that injuries of the cannibal may be neglected as well.

When parents and offspring live close together, a cannibalistic individual has a higher chance to consume its own offspring than that of an arbitrary individual. We ignore such a consequence of spatial structure and pretend that the world is well-mixed.

The (dis) advantages at the i-level resulting from cannibalism are as follows. First, a juvenile has of course a chance of being eaten by a conspecific adult, whereas an adult receives additional energy when cannibalizing a juvenile. But an adult also faces a possible disadvantage related to optimal foraging: perhaps the handling time and digestion capacity spent on intraspecific prey are better spent on other sources of food?

What is the effect at the population level resulting from these mechanisms? If positive aspects at the individual level do not play a role, one expects of course negative effects at the population level. An early and detailed example of such a negative effect is given in (Botsford 1981). In this paper cannibalism is modeled as a density dependent phenomenon and energy gain for the predator is not taken into account. It is analyzed how, at a low population level, the effect of population density on individual survival to recruitment (e.g. via cannibalistic predation) can, under the assumption that low population levels result in an increase in individual growth rate, contribute to the maintenance of a low population level. (In fact this cannibalism model is the first in which bistability is found).

As shown in several papers, however, see (Van den Bosch et al. 1988), (Henson 1995), (Van den Bosch and Gabriel 1997), (Diekmann 1999) and (Diekmann et al. 2003), when taking energy gain of the cannibal into account, the net effect at the p-level may be positive, in the sense that the population persists under food conditions such that, without cannibalism, the population would go extinct (the name "life boat mechanism" suggests, perhaps, that such food conditions occur only every now and then). The key point is that juveniles have access to food which is too small (or otherwise inaccessible) for the adults themselves. So, in a sense, the juveniles form part of the foraging strategy of the adults.

In all earlier work on the life boat mechanism that we are aware of, the juvenile food and the non-cannibalistic adult food were taken constant, i.e., not influenced by the population itself through consumption. Moreover, in many models juvenile food was not considered explicitly. In the present paper we distinguish between juvenile and adult food explicitly and incorporate that their steady state levels are influenced via consumption by the size and composition of the population. In loose terms our main conclusion is that the life boat mechanism manifests itself when the adult food is the limiting resource, while being irrelevant when the juvenile food is the limiting resource.

Another main theme of this paper is, that from the point of view of evolution by natural selection, the life boat mechanism is not what counts. Indeed, as the theory of Adaptive Dynamics (Metz et al. 1992, 1996), (Dieckmann and Law 1996), (Geritz et al. 1997, 1998) and (Diekmann 2004) tells us, we should investigate whether a (slightly) cannibalistic small subpopulation starts to grow exponentially in the environmental (= food) conditions as set by the non-cannibalistic (so called "resident") population. Phrased this manner, the question concerns the evolutionary onset of cannibalism. After it has been answered, further questions arise naturally: what degree of cannibalism should we expect? What does, apart from physiological constraints due to size-size incompatibility, determine the size-window in which individuals are vulnerable to intraspecific predation by an individual of a given size? Etcetera. As we shall show, the "evolutionary onset" question is easier to answer than the "lifeboat" question: standard optimal foraging arguments suffice. The reason is that evolution is short sighted: only immediate gains and losses count and not how the world will be after the successful mutant has ousted the former resident.

Yet, fortunately, the two themes do not clash. In, once again, loose terms, the conclusion of the analysis in adaptive dynamics spirit is, that cannibalism will originate if adult food is the limiting resource, while it will not, if juvenile food is the limiting resource. So, despite the fact that the quantitative details of the "life boat" condition and the "evolutionary onset" condition differ substantially, we can say, that at a qualitative level the population advantages of cannibalism manifest themselves exactly when the individual advantages lead to cannibalism. When interpreted in a certain way, the life boat population phenomenon gives a clue concerning the evolutionary advantages of cannibalistic clans.

Exploiting the "only one state at birth" feature, we rewrite the steady state problem as a nonlinear system of equations in the so-called environmental interaction variable I and the population birth rate c. The technical basis for the bifurcation analysis that we outline at the beginning of Section 4, is provided in more generality in *Steady state analysis for a size structured cannibalism model with two dynamic resources*, which is a chapter in the PhD thesis of the first author (Getto, thesis) and available on request. In the latter one finds an extension of the bifurcation analysis in (Diekmann et al. 2003) to an infinite-dimensional environmental interaction variable I, as appearing in the parametrization of (Claessen and de Roos 2002) or (Claessen 2002), and two dynamic resources.

The bifurcation parameter that we consider is the position along a curve in the two parameter plane of the carrying capacities of, respectively, juvenile and adult food.

2. The model formulation

In an attempt to bring out the bare essentials, we sacrifice much of the generality of the model proposed in (Getto, thesis). In particular we assume here that juveniles, and only juveniles, grow and that adults, and only adults, reproduce. Only adults cannibalise and they can only cannibalise juveniles of suitable sizes. A generality we allow for, however, is the existence of two dynamic standard food sources, one

for juveniles and one for adults. So juveniles compete for food among themselves and so do adults. But adults that are cannibalistic do have an additional source of food: the juveniles.

We assume that every individual is born with size x_b and turns into an adult upon reaching size x_A. Juveniles of size x experience a force of mortality $\mu_1(x)$ and, possibly, an additional force of mortality due to cannibalism. Adults experience a force of mortality μ_2.

We now specify our assumptions on individual growth, reproduction and maintenance in terms of a partitioning of the individual's energy budget. More precisely, we use a so-called net-assimilation model, in contrast to a net-reproduction model, see (Kooijman 2000) for details (also for the case where growth and reproduction occur "simultaneously"). We denote by Z_1 the density/concentration of juvenile food and by Z_2 that of adult food. Incorporating a Holling Type II functional response, a juvenile individual of size x gains energy at rate

$$\frac{E_1(x)C_1(x)Z_1}{1 + H_1(x)C_1(x)Z_1},\tag{2.1}$$

where C_1 is the size-specific attack rate, H_1 the size-specific handling time (or, alternatively, a measure for the digestive capacity involved) and E_1 the amount of energy gained from a unit of food (which is allowed to be size-specific).

We assume that maintenance costs are proportional to size and that, in the case of juveniles, all remaining energy is scheduled to growth. Hence we have

$$\frac{dx}{da} = \eta_1 \left(\frac{E_1(x)C_1(x)Z_1}{1 + H_1(x)C_1(x)Z_1} - \zeta_1 x \right),\tag{2.2}$$
$$x(0) = x_b$$

to describe how the size x of a juvenile individual changes with its age a (here η_1 takes care of converting energy units into size units and ζ_1 is the amount of energy per unit of time and unit of size needed for maintenance). Implicitly we here assume that the energy ingested exceeds what is needed for maintenance, which is always true in a nontrivial equilibrium.

Analogously, a non-cannibalistic adult gains energy at rate

$$\frac{E_2 C_2 Z_2}{1 + H_2 C_2 Z_2}\tag{2.3}$$

and, after paying for maintenance, uses this energy for reproduction. In other words, a non-cannibalistic adult produces offspring at rate

$$\eta_2 \left(\frac{E_2 C_2 Z_2}{1 + H_2 C_2 Z_2} - \zeta_2 x_A \right).\tag{2.4}$$

We assume that food is produced at a constant rate and that decay of food is a linear process. So in the absence of consumption the food density/concentration would

stabilize at a certain level, which we denote by, respectively, K_1 (juvenile food) and K_2 (adult food). If we now include the effect of consumption we arrive at equations

$$\frac{dZ_1}{dt} = r_1(K_1 - Z_1) - \int_{x_b}^{x_A} \frac{C_1(x)Z_1}{1 + H_1(x)C_1(x)Z_1} n(\cdot, x)dx, \tag{2.5}$$

$$\frac{dZ_2}{dt} = r_2(K_2 - Z_2) - \frac{C_2 Z_2}{1 + H_2 C_2 Z_2} N_A(\cdot) \tag{2.6}$$

to describe the dynamics of the food concentrations. Here $n(t, \cdot)$ is the size-density of juveniles at time t and $N_A(t)$ the density/number of adults at time t.

To incorporate the effects of cannibalism we adjust two model components: the juvenile death rate and the adult energy intake rate. The quantities C, H and E provided with an index y refer to a victim of size y. When adults are cannibalistic we replace (2.3) by

$$\frac{E_2 C_2 Z_2 + \int_{x_b}^{x_A} E_y C_y n(\cdot, y)dy}{1 + H_2 C_2 Z_2 + \int_{x_b}^{x_A} H_y C_y n(\cdot, y)dy} \tag{2.7}$$

and adapt (2.4) and (2.6) (the latter only in the denominator) accordingly, while putting the per capita death rate of juveniles of size x equal to

$$\mu_1(x) + \frac{C_x N_A(\cdot)}{1 + H_2 C_2 Z_2 + \int_{x_b}^{x_A} H_y C_y n(\cdot, y)dy}. \tag{2.8}$$

3. The steady state equations for a noncannibalistic population

We first consider a non-cannibalistic population. Introducing (cf. (2.2)) the individual growth rate

$$g(x, Z_1) = \eta_1 \left(\frac{E_1(x)C_1(x)Z_1}{1 + H_1(x)C_1(x)Z_1} - \zeta_1 x \right), \tag{3.1}$$

we can express the probability $\Pi(Z_1)$, that a newborn individual survives till it reaches size x_A and becomes adult, given a constant (in time) food concentration Z_1, as

$$\Pi(Z_1) = \exp\left(-\int_{x_b}^{x_A} \frac{\mu_1(y)}{g(y, Z_1)}dy \right). \tag{3.2}$$

Once turned adult, the individual lives for an expected period $\frac{1}{\mu_2}$ of time, during which it produces offspring at the rate (2.4) when adult food has the constant (in time) concentration Z_2. So the expected number of offspring produced by an individual just turned adult equals

$$R_A(Z_2) = \frac{1}{\mu_2}\eta_2 \left(\frac{E_2 C_2 Z_2}{1 + H_2 C_2 Z_2} - \zeta_2 x_A \right). \tag{3.3}$$

Consequently the expected number of offspring produced by a newborn individual equals

$$R_0(Z_1, Z_2) = \Pi(Z_1)R_A(Z_2). \tag{3.4}$$

A first requirement for steady state is that the two food concentrations are such that

$$R_0(Z_1, Z_2) = 1. \tag{3.5}$$

If, under such conditions, the steady population birth rate equals c, the stable juvenile size distribution is described by the density function

$$n(x) = \frac{c}{g(x, Z_1)} \exp\left(-\int_{x_b}^{x} \frac{\mu_1(y)}{g(y, Z_1)} dy\right). \tag{3.6}$$

Therefore, the rate $g(x_A, Z_1)n(x_A)$ at which adults are recruited, equals $c\Pi(Z_1)$ and we have

$$N_A = \frac{c\Pi(Z_1)}{\mu_2}. \tag{3.7}$$

The second and third requirements for steady state are, that the left hand sides of (2.5) and (2.6) are equal to zero, therefore, using (3.6) and (3.7), we find

$$0 = r_1(K_1 - Z_1) - cZ_1 \int_{x_b}^{x_A} \frac{C_1(x)}{1 + H_1(x)C_1(x)Z_1} \frac{1}{g(x, Z_1)} e^{-\int_{x_b}^{x} \frac{\mu_1(y)}{g(y, Z_1)} dy} dx, \tag{3.8}$$

$$0 = r_2(K_2 - Z_2) - \frac{C_2 Z_2}{1 + H_2 C_2 Z_2} \frac{c\Pi(Z_1)}{\mu_2}. \tag{3.9}$$

Together (3.5), (3.8) and (3.9) are three equations in the three unknowns Z_1, Z_2 and c. For any solution (with c, $Z_i \geq 0$) the steady population size and composition is given by (3.6), (3.7), while the Z_i are the steady food levels. By eliminating c from (3.8), (3.9) one reduces the system to two equations in the two unknowns Z_1 and Z_2. Each equation defines a curve in the (Z_1, Z_2) -plane and solutions are precisely the points of intersection of the two curves.

4. The steady state equations for a cannibalistic population

For a cannibalistic population the situation becomes more complicated. Yet, following the methodology introduced in (Diekmann et al. 2003), we can derive six equations in six unknowns. The key idea is to rewrite (2.7) and (2.8) as, respectively,

$$\frac{E_2 C_2 Z_2 + I_1}{1 + H_2 C_2 Z_2 + I_2} \tag{4.1}$$

and

$$\mu_1(x) + \frac{C_x I_3}{1 + H_2 C_2 Z_2 + I_2}, \tag{4.2}$$

introducing

$$I_1 := \int_{x_b}^{x_A} E_y C_y n(y) dy, \tag{4.3}$$

$$I_2 := \int_{x_b}^{x_A} H_y C_y n(y) dy, \tag{4.4}$$

$$I_3 := N_A.$$

The two following points are crucial:

1) The dependence on the infinite-dimensional parameter $n = n(y)$ in (2.7) and (2.8) is replaced by a dependence on the three dimensional variable (I_1, I_2, I_3) in (4.1) and (4.2). So the I_i capture exactly the feedback of the population on the individuals. We call them *interaction variables* and we call the vector I *environmental condition* (where one should realize that we do not explicitly consider aspects of the "true" environment that are not in one way or another under the influence of feedback).
2) The I_i are chosen such that their dependence on n in (4.3) and (4.4) is linear.

A consequence of point 1) is that when constructing the expected lifetime offspring R_0 from the energy uptake (4.1) and mortality (4.2) we obtain a condition for steady state of the form

$$R_0(I) = 1, \tag{4.5}$$

(see (4.11) below), i.e., an equation in a finite number of variables. To see the advantage resulting from 2), note first that the expression (3.6) for the juvenile size density is replaced by

$$n(x) = \frac{c}{g(x, Z_1)} \exp\left(-\int_{x_b}^{x} \left(\mu_1(y) + \frac{C_y I_3}{1 + H_2 C_2 Z_2 + I_2}\right) \frac{1}{g(y, Z_1)} dy\right) \tag{4.6}$$

and (3.7) now reads

$$N_A = I_3 = \frac{c \Pi^c(Z_1, Z_2, I_2, I_3)}{\mu_2}, \tag{4.7}$$

where Π^c is defined in (4.9) below and the superindex c refers to cannibalism (and not to the population birth rate). Note in particular that both n and I_3 depend linearly on c. If we plug (4.6) into (4.3) and (4.4) the same applies to I_1 and I_2. Thus we obtain equations of the form

$$I_i = cF(Z_1, Z_2, I_1, I_2, I_3), \quad i = 1, 2, 3. \tag{4.8}$$

We will supplement the four equations (4.5) and (4.8) by two more equations expressing that the food concentrations Z_1 and Z_2 should be steady. Thus we obtain six equations in six unknowns, c, I_1, I_2, I_3 and Z_1 and Z_2. In summary, we have arrived at a finite dimensional problem, where the linear c-dependence in (4.8) is tailor-made for the bifurcation analysis that we will perform in Section 6.

The steady state is completely determined by a steady environmental condition I and a population birth rate c, see (4.6) and (4.7). The equations that these quantities should satisfy are consistency conditions. Solving the steady state problem can thus be interpreted as specifying an environment I and a "population" c such that the basic reproduction number under this environmental condition equals one and such that the population consistently determines the environment.

One of the remaining tasks is hence to model R_0 and in order to do so observe, that the analogue of (3.2) is

$$\Pi^c(Z_1, Z_2, I_2, I_3) = \exp\left(-\int_{x_b}^{x_A}\left(\mu_1(x) + \frac{C_x I_3}{1 + H_2 C_2 Z_2 + I_2}\right)\frac{1}{g(x, Z_1)}dx\right)$$

(4.9)

and the analogue of (3.3) is

$$R_A^c(Z_2, I_1, I_2) = \frac{1}{\mu_2}\eta_2\left(\frac{E_2 C_2 Z_2 + I_1}{1 + H_2 C_2 Z_2 + I_2} - \zeta_2 x_A\right).$$

(4.10)

Thus, (3.5) becomes

$$R_0^c(Z_1, Z_2, I_1, I_2, I_3) = 1,$$

(4.11)

where by definition

$$R_0^c(Z_1, Z_2, I_1, I_2, I_3) = \Pi^c(Z_1, Z_2, I_2, I_3)R_A^c(Z_2, I_1, I_2).$$

(4.12)

The conditions for steady food levels are

$$0 = r_1(K_1 - Z_1) - cZ_1\int_{x_b}^{x_A}\frac{C_1(x)}{1 + H_1(x)C_1(x)Z_1}\frac{1}{g(x, Z_1)}$$
$$\times \exp\left(-\int_{x_b}^{x}\left(\mu_1(y) + \frac{C_y I_3}{1 + H_2 C_2 Z_2 + I_2}\right)\frac{1}{g(y, Z_1)}dy\right)dx, \quad (4.13)$$

$$0 = r_2(K_2 - Z_2) - \frac{C_2 Z_2 I_3}{1 + H_2 C_2 Z_2 + I_2}.$$

(4.14)

The equations (4.11), (4.13) and (4.14) are supplemented by the so called feedback relations (4.7) and

$$I_1 = c\int_{x_b}^{x_A}\frac{E_x C_x}{g(x, Z_1)}$$
$$\times \exp\left(-\int_{x_b}^{x}\left(\mu_1(y) + \frac{C_y I_3}{1 + H_2 C_2 Z_2 + I_2}\right)\frac{1}{g(y, Z_1)}dy\right)dx, \quad (4.15)$$

$$I_2 = c\int_{x_b}^{x_A}\frac{H_x C_x}{g(x, Z_1)}$$
$$\times \exp\left(-\int_{x_b}^{x}\left(\mu_1(y) + \frac{C_y I_3}{1 + H_2 C_2 Z_2 + I_2}\right)\frac{1}{g(y, Z_1)}dy\right)dx. \quad (4.16)$$

Together, (4.11) and (4.7)–(4.16) constitute six equations in the six unknowns c, Z_1, Z_2, I_1, I_2 and I_3.

5. The evolutionary onset of cannibalism

Suppose, that the food levels are set at constant values by a non-cannibalistic population. Suppose a cannibalistic mutant enters the scene and suppose that it reproduces clonally. Does it generate an exponentially growing clan or does its clan go extinct? Ignoring the subtleties of demographic stochasticity, the answer is provided by the quantity $R_0^c(Z_1, Z_2, I_1, I_2, 0)$ defined by (4.12), in the sense that exponential growth sets in if and only if it exceeds one. The fact that we have put I_3 equal to zero correponds to the assumption, that as long as the clan is small relative to the population at large, the chance that its juvenile members fall victim to cannibalism is negligible. Therefore, the only possible disadvantage a cannibalistic invader faces, is that while cannibalising it loses time it could spend on a possibly more nutritious recource. Likewise one should put $I_3 = 0$ in the defining expressions (4.15), (4.16) for I_1 and I_2. As a result we have explicit formulas for I_1 and I_2 in terms of c, Z_1 and Z_2. Consequently, $R_0^c(Z_1, Z_2, I_1, I_2, 0)$ is a computable number, once the c, Z_1 and Z_2 are specified.

Now note, that from (4.9), it follows that $\Pi^c(Z_1, Z_2, I_2, 0)$ is independent of I_2 and Z_2 and, in fact, equal to $\Pi(Z_1)$ defined in (3.2). Hence $R_0^c(Z_1, Z_2, I_1, I_2, 0) > 1$ if and only if

$$R_A^c(Z_2, I_1, I_2) > R_A(Z_2) \tag{5.1}$$

(since $R_0^c(Z_1, Z_2, 0, 0, 0) = \Pi(Z_1)R_A(Z_2) = 1$). Therefore, the cannibalistic subpopulation will start to grow exponentially in the environmental conditions as set by the non-cannibalistic resident if and only if

$$\frac{E_2C_2Z_2 + I_1}{1 + H_2C_2Z_2 + I_2} > \frac{E_2C_2Z_2}{1 + H_2C_2Z_2}. \tag{5.2}$$

This simply means, that the cannibalistic energy intake and handling time should compensate each other in such a way, that the "overall" energy intake rate of a cannibal exceeds the one of a non-cannibal. Now, inequality (5.2) can also be written as

$$\frac{I_1}{I_2} > \frac{E_2C_2Z_2}{1 + H_2C_2Z_2}, \tag{5.3}$$

which means that the ratio of cannibalism related energy intake and cannibalism related handling time should exceed the average energy intake rate of non-cannibalistic individuals. Hence, we deduced the standard optimal foraging criterion. A necessary condition for (5.3) to hold is, that

$$\frac{E_y}{H_y} > \frac{E_2C_2Z_2}{1 + H_2C_2Z_2}, \tag{5.4}$$

for at least some $y \in (x_b, x_A)$. This is simply a size-specific version of the criterion. If it is satisfied, one can satisfy (5.3) by restricting C_y such that it is positive only for y for which (5.4) holds (whether or not this is a physiologically feasible option is another matter).

We conclude that the evolutionary onset of cannibalism can be understood via optimal foraging considerations. (And, actually, so is a further intensification of cannibalistic activity: a *rare* type of individual does not suffer from the extra mortality it generates by *direct* interaction, since this is a quadratic effect).

6. Population level effects

The *lifeboat mechanism* refers to the possibility that the steady state equations, i.e., (4.11), (4.7)–(4.16), may have a solution for values of the carrying capacity parameters K_1 and K_2 for which (3.5), (3.8), (3.9) does not have a solution, i.e., values where, as opposed to a cannibalistic population, a noncannibalistic population can not persist. To investigate this possibility, we focus on a neighbourhood of the critical set in the (K_1, K_2)-plane, where $R_0 = 1$ for a population which invades the virgin environment in which both food levels are at their carrying capacities. Since, as indeed should be the case,

$$R_0^c(Z_1, Z_2, 0, 0, 0) = R_0(Z_1, Z_2), \tag{6.1}$$

the critical set is the same for the non-cannibalistic as for the cannibalistic population. It is defined by the equation

$$R_0(K_1, K_2) = 1. \tag{6.2}$$

Since (cf. (3.4)) $R_0(K_1, K_2)$ is the product of two monotone functions of a single variable, the critical set has the qualitative features depicted in Figure 1. For the noncannibalistic population, a steady state can only exist, if (K_1, K_2) lies above the critical curve, because from (3.8) and (3.9) we see, that $c > 0$ implies $Z_i < K_i$ for $i \in \{1, 2\}$ whence $\Pi(K_1) > \Pi(Z_1)$ and $R_A(K_2) > R_A(Z_2)$ and, consequently,

$$R_0(K_1, K_2) > R_0(Z_1, Z_2) = 1.$$

For the cannibalistic population it is not as simple to determine the set of (K_1, K_2) values for which a non-trivial steady state (i.e., $c > 0$) exists. Our strategy is to concentrate on small values of c and to do a perturbation analysis. More precisely, in the six equations (4.11), (4.7)–(4.16), we shall consider $I = (I_1, I_2, I_3)$, $Z = (Z_1, Z_2)$ and K_2 as the unknowns and K_1 and c as parameters. For $c = 0$ we have the one parameter curve of solutions $I = 0$, $Z = K$, $K_2 = \Phi_0(K_1)$, where Φ_0 is the function whose graph is depicted in Figure 1 or, in other words

$$\Phi_0(K_1) := R_A^{-1}\left(\frac{1}{\Pi(K_1)}\right). \tag{6.3}$$

Now, fix K_1 and look for solutions of the form

$$\begin{aligned}
I &= ck(K_1) + o(c), \\
Z &= K + c\Theta(K_1) + o(c), \\
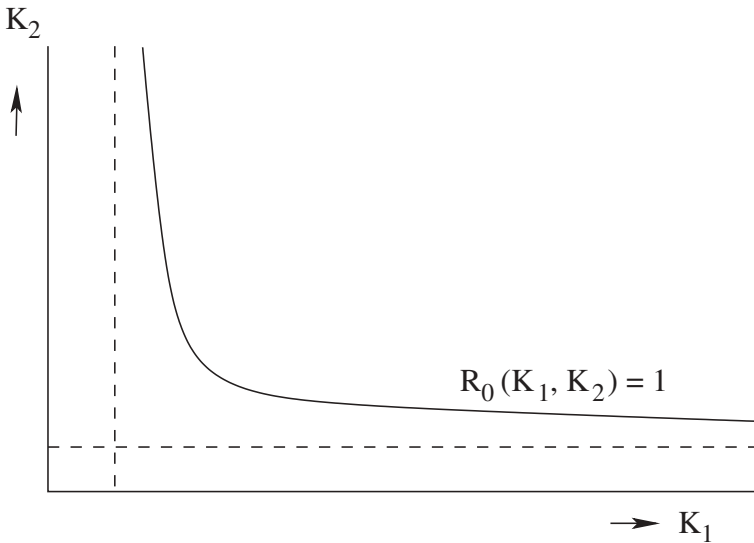K_2 &= \Phi_0(K_1) + c\Phi_1(K_1) + o(c),
\end{aligned} \tag{6.4}$$

Fig. 1. Graph of the critical curve $R_0(K_1, K_2) = 1$. For parameters in the region above the curve, a population introduced in the virgin environment $Z = K$ starts growing exponentially, while for parameters in the region below the curve, a small population goes extinct. The asymptotic values are defined as the solutions of $\lim_{K_1 \uparrow \infty} \Pi(K_1) R_A(K_2) = 1$, $\lim_{K_2 \uparrow \infty} \Pi(K_1) R_A(K_2) = 1$.

where $o(c)$ denote the higher order terms in the small parameter c. As emphasized in (Diekmann et al. 2003), our way of pre-processing the steady state problem has the advantage, that k and Θ are easily computed. Indeed, from, respectively, (4.15), (4.16) and (4.7), we deduce

$$k(K_1) = \begin{pmatrix} \int_{x_b}^{x_A} \frac{E_x C_x}{g(x, Z_1)} e^{- \int_{x_b}^{x} \frac{\mu_1(y)}{g(y, Z_1)} dy} dx \\ \int_{x_b}^{x_A} \frac{H_x C_x}{g(x, Z_1)} e^{- \int_{x_b}^{x} \frac{\mu_1(y)}{g(y, Z_1)} dy} dx \\ \frac{\Pi(K_1)}{\mu_2} \end{pmatrix}. \tag{6.5}$$

Likewise, we deduce from (4.13) and (4.7), plugged into (4.14), that

$$\Theta(K_1) = - \begin{pmatrix} \frac{K_1}{r_1} \int_{x_b}^{x_A} \frac{C_1(x)}{1 + H_1(x) C_1(x) K_1} \frac{1}{g(x, K_1)} e^{- \int_{x_b}^{x} \frac{\mu_1(y)}{g(y, K_1)} dy} dx \\ \frac{1}{r_2} \frac{C_2 \Phi_0(K_1)}{1 + H_2 C_2 \Phi_0(K_1)} \frac{\Pi(K_1)}{\mu_2} \end{pmatrix}. \tag{6.6}$$

It remains to determine $\Phi_1(K_1)$. To do so, in (6.4) we plug the third equation into the second, then the first two into (4.11) and finally expand up to first order with respect to c. This way, we obtain the equation

$$\frac{\partial R_0^c}{\partial Z_2} \Phi_1(K_1) + \frac{\partial R_0^c}{\partial Z} \Theta(K_1) + \frac{\partial R_0^c}{\partial I} k(K_1) = 0, \tag{6.7}$$

which is linear in Φ_1, Θ and k (note that the last two terms are vector products). It can be solved for Φ_1, since monotonicity guarantees, that $\frac{\partial R_0^c}{\partial Z_2} \neq 0$ (note that, for the same reason, our formal solution is justified by the Implicit Function Theorem).

Since $\frac{\partial R_0^c}{\partial Z_2} > 0$, we deduce that

$$sign\ \Phi_1 = -sign\left(\frac{\partial R_0^c}{\partial Z}\Theta + \frac{\partial R_0^c}{\partial I}k\right). \tag{6.8}$$

Since $K_2 \longrightarrow R_0(K_1, K_2)$ is monotonically increasing, it follows from the last equation of (6.4), that the small-c-level steady state solution exists in the region where

$$R_0(K_1, K_2) < 1,$$

if and only if $sign\ \Phi_1 < 0$. Therefore we will say from now on, that the *life boat mechanism works when* $sign\ \Phi_1 < 0$. Note, that by speaking about *small-c-level* solutions, we emphasize that this is a local property: we refer to (Van den Bosch et al. 1988) for an example of more complicated global behaviour.

7. Elaboration of the criteria

In this section we consider (5.3) and (6.8) in more detail, both separately and to uncover their interrelationship.

At the critical curve $K_2 = \Phi_0(K_1)$, the left hand side of (5.3) reduces to

$$\frac{\int_{x_b}^{x_A} \frac{E_y C_y}{g(y, K_1)} e^{-\int_{x_b}^y \frac{\mu_1(x)}{g(x, K_1)}dx} dy}{\int_{x_b}^{x_A} \frac{H_y C_y}{g(y, K_1)} e^{-\int_{x_b}^y \frac{\mu_1(x)}{g(x, K_1)}dx} dy}$$

and therefore the no-onset condition, i.e., the reverse of (5.3), can be formulated as

$$\int_{x_b}^{x_A} \left(\frac{E_y}{H_y} - \frac{E_2 C_2 \Phi_0(K_1)}{1 + H_2 C_2 \Phi_0(K_1)}\right) \frac{H_y C_y}{g(y, K_1)} e^{-\int_{x_b}^y \frac{\mu_1(x)}{g(x, K_1)}dx} dy < 0. \tag{7.1}$$

Accordingly, a sufficient no-onset condition is, that

$$\frac{E_y}{H_y} < \frac{E_2 C_2 \Phi_0(K_1)}{1 + H_2 C_2 \Phi_0(K_1)}, \tag{7.2}$$

for all y which correspond to vulnerable juveniles (or, in mathematical jargon, for all y in the support of C_y).

As Φ_0 is a decreasing function, we conclude that,

if the sufficient no-onset condition (7.2) *is satisfied for some* K_1, *it is satisfied for all smaller values of* K_1 *(nota bene that, along the curve,* K_1 *and* K_2 *are coupled!).*

If we additionally assume, that $\frac{E_y}{H_y}$ is the same for all vulnerable juveniles, we can say a little more. First, note that $\Phi_0(K_1)$ tends, for $K_1 \longrightarrow \infty$, to the value of

Z_2, which makes R_A equal to $\frac{1}{\Pi(\infty)}$ (recall Figure 1). Therefore, we deduce from (3.3), that

$$\frac{E_2 C_2 \Phi_0(K_1)}{1 + H_2 C_2 \Phi_0(K_1)} = \zeta_2 x_A + \frac{\mu_2}{\eta_2 \Pi(\infty)}. \tag{7.3}$$

Thus, a necessary condition for onset of cannibalism is

$$\frac{E_y}{H_y} > \zeta_2 x_A + \frac{\mu_2}{\eta_2 \Pi(\infty)} \tag{7.4}$$

for vulnerable juveniles.

At the other extreme, where K_1 tends to the lower boundary of the interval on which Φ_0 is defined, we have $\Phi_0(K_1) \longrightarrow \infty$. Therefore, if

$$\frac{E_y}{H_y} > \frac{E_2}{H_2}, \tag{7.5}$$

the necessary onset condition is satisfied for all values of K_1, for which the population can persist. Note, that implicitly we have assumed, that

$$\frac{E_2}{H_2} > \zeta_2 x_A + \frac{\mu_2}{\eta_2 \Pi(\infty)},$$

since otherwise this set of K_1 values would be empty. Hence, (7.5) is indeed a more severe condition than (7.4). The meaning of (7.5) is, that cannibalistic food is more profitable than standard adult food. If (7.5) is not satisfied, but (7.4) is, we show that there is along the critical curve exactly one point, such that onset is impossible to the left, but possible to the right (see Figure 2).

Above the critical curve, the inequality (5.2) can be rewritten as

$$\int_{x_b}^{x_A} \left(\frac{E_y}{H_y} - \frac{E_2 C_2 Z_2}{1 + H_2 C_2 Z_2} \right) \frac{H_y C_y}{g(y, Z_1)} e^{-\int_{x_b}^{y} \frac{\mu_1(x)}{g(x, Z_1)} dx} dy > 0. \tag{7.6}$$

Still assuming that $\frac{E_y}{H_y}$ is constant and that (7.4), but not (7.5), is satisfied, we will obtain a well-defined critical Z_2 level, at which the left hand side of (7.6) switches sign. More precisely, let Z_2^c denote the unique solution of the equation

$$\frac{E_y}{H_y} = \frac{E_2 C_2 Z_2}{1 + H_2 C_2 Z_2}, \tag{7.7}$$

then onset is impossible, if $Z_2^{ss} > Z_2^c$ and possible if $Z_2^{ss} < Z_2^c$, where Z_2^{ss} is the steady state adult food level. Explicitly, from (7.7) we get

$$Z_2^c = \frac{E_y}{C_2(E_2 H_y - H_2 E_y)}. \tag{7.8}$$

Our next aim is to find the curve in the (K_1, K_2)-parameter plane, at which $Z_2^{ss} = Z_2^c$. We shall find, that this is a straight line with positive slope, starting at the point on the critical curve described above and defined (uniquely) by $\Phi_0(K_1) = Z_2^c$.
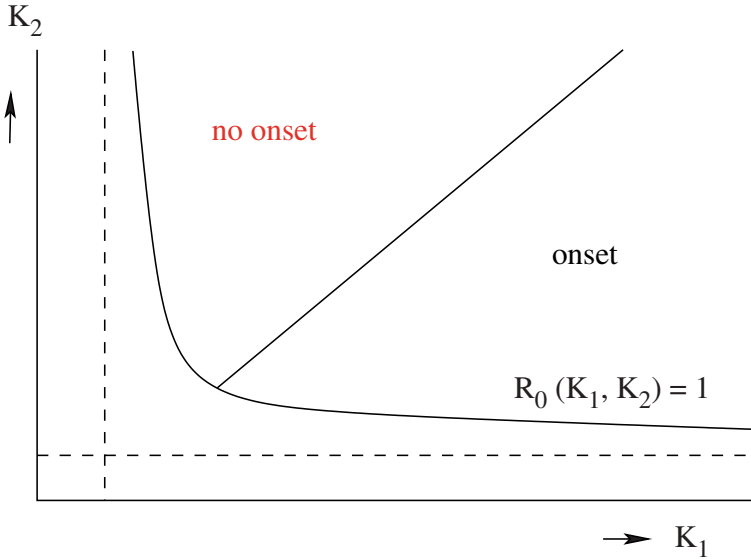
Fig. 2. Subdivision of the parameter plane in the region in which onset of cannibalism is impossible and the complementary region in which onset of cannibalism is possible.

If the level of Z_2 is fixed a priori, we can use (3.5) to determine the level of Z_1. Thus, define

$$Z_1^c = \Pi^{-1}\left(\frac{1}{R_A(Z_2^c)}\right). \tag{7.9}$$

Next, use (3.9) to determine c. The result is

$$c = r_2 \frac{E_2}{E_y} R_A(Z_2^c)\mu_2 H_y(K_2 - Z_2^c). \tag{7.10}$$

Finally, substituting (7.9) and (7.10) into (3.8), we find a linear equation relating K_1 and K_2. In the equation, the coefficient of K_1 is positive and the coefficient of K_2 is negative, therefore the graph of K_2 as a function of K_1 is a straight line with positive slope. Monotonicity arguments guarantee that onset is possible to the right of this line and impossible to the left (see Figure 2).

We now turn our attention to (6.8) and first make the following sign observations:

$$\frac{\partial R_0^c}{\partial Z_1} > 0, \quad \frac{\partial R_0^c}{\partial Z_2} > 0, \quad \frac{\partial R_0^c}{\partial I_1} > 0, \quad \frac{\partial R_0^c}{\partial I_2} < 0, \quad \frac{\partial R_0^c}{\partial I_3} < 0,$$

where all quantities are evaluated at the critical curve, such that $Z_1 = K_1$, $Z_2 = \Phi_0(K_1)$ and $I = 0$. In addition, from (6.5) and (6.6) one sees that

$$\theta_i < 0, \quad k_i > 0,$$

so only

$$\frac{\partial R_0^c}{\partial I_1} k_1$$

(corresponding to extra energy intake of adults) gives a positive contribution to $\frac{\partial R_0^c}{\partial Z}\theta + \frac{\partial R_0^c}{\partial I}k$, all other terms are negative. The term $\frac{\partial R_0^c}{\partial I_2}k_2$ corresponds to the diminishing of the energy intake of standard food due to time/digestion capacity spent on intraspecific predation, $\frac{\partial R_0^c}{\partial I_3}k_3$ to the decreased survival probability due to cannibalistic predation pressure and the $\frac{\partial R_0^c}{\partial Z_i}\Theta_i$ to the increase of energy intake with standard food. Now note that from (4.12), (4.9) and (4.10) one computes

$$\frac{\partial R_0^c}{\partial I_1}k_1 + \frac{\partial R_0^c}{\partial I_2}k_2$$
$$= \frac{\eta_2 \Pi(K_1)}{\mu_2(1 + H_2 C_2 \Phi_0(K_1))}$$
$$\int_{x_b}^{x_A} \left(\frac{E_y}{H_y} - \frac{E_2 C_2 \Phi_0(K_1)}{1 + H_2 C_2 \Phi_0(K_1)}\right) \frac{H_y C_y}{g(y, K_1)} e^{-\int_{x_b}^{y} \frac{\mu_1(x)}{g(x,K_1)}dx} dy. \quad (7.11)$$

Comparison with (7.1) and/or (7.2) immediately leads to the conclusion, that

the life boat mechanism can only work when onset of cannibalism is possible.

Since the quantity in (7.11) needs to be sufficiently positive to compensate the negative contributions of the other three terms in

$$\frac{\partial R_0^c}{\partial Z}\theta + \frac{\partial R_0^c}{\partial I}k$$

(in order for Φ_1 to be negative; recall (6.8)), we see clearly, that a more severe condition needs to be satisfied for the life boat mechanism to work, than for mere onset of cannibalism. Note, that unlike in the limit $K_2 \longrightarrow \infty$, for $K_1 \longrightarrow \infty$ the sign of Φ is not apparent, without further assumptions. We suspect, that the quantity Φ_1 switches sign at most once along the critical curve, but we did not manage to prove this. A sufficient condition for the lifeboat mechanism, however, can be given, by observing, that $\frac{E_y}{H_y}$ (assumed constant) appears only once in (7.11) and not at all in the other terms of

$$\frac{\partial R_0^c}{\partial Z}\theta + \frac{\partial R_0^c}{\partial I}k.$$

It follows that the lifeboat mechanism manifests itself for sufficiently large $\frac{E_y}{H_y}$. We refer to (Diekmann et al. 2003) and (Getto, thesis) for a further elaboration of the life boat condition in the simpler setting of constant food availability and for a precise biological interpretation of the condition in such a setting.

8. Concluding remarks

In the context of a size structured population model with two dynamic food sources, one for juveniles and one for adults, we have investigated both the conditions for the evolutionary onset of cannibalism and the condition for persistence of a cannibalistic population, where it would go extinct in the absence of cannibalism. At a qualitative level the conditions agree, in quantitative detail they differ considerably. The common denominator is, that cannibalism, in the form that the big adults eat the small juveniles, pays when adult food is limiting and does not pay when juvenile food is limiting.

Our adaptive dynamics approach focussed on steady state attractors, mainly since these are amenable to analysis with pencil and paper. We do think, however, that the distinction between onset of cannibalism and the life boat mechanism might become negligible when food fluctuates. To verify this idea one could, for instance, repeat the analysis of this paper for the situation that one or both of the parameters K_1 and K_2 is a periodic function of time. Another possibility is, to assume that reproduction is concentrated in a short period of the year. Even with constant K the food levels will then change during the year, due to the physiological development of the cohorts.

In a recent review on the population dynamic theory of size-dependent cannibalism, (Claessen et al. 2004) distinguished four critical aspects of cannibalism: 1) victim mortality, 2) energy extraction from victims, 3) size dependence and 4) competition. The size dependence of the cannibalistic interaction results from that cannibals are usually larger than their victims, while competition is implicated because cannibals and victims are the same species and may hence share common resources. Of the 30 different models of cannibalistic interactions reviewed, all accounted for victim mortality, but only 50% of them accounted for the direct positive effect of energy gain from killing and eating a conspecific. Few models accounted for all four aspects of cannibalism. At the population level different types of possible responses due to cannibalism were distinguished, among which the occurrence of multiple equilibria and the life boat effect. (Cushing 1991) pointed out already that the interplay between positive and negative effects of cannibalism can result in multiple steady states. Energy extraction from victims is the direct, positive effect, but indirect, positive effects occur as well, as cannibalism may reduce intraspecific competition and hence benefit growth and reproduction. (Claessen et al. 2004) argue that the life boat effect results from the disbalance between the direct, positive effect of energy extraction and the direct, negative effect of imposing victim mortality. The model we analyze does account for victim mortality, energy extraction and size-dependence of the cannibalistic interaction. The fourth aspect of cannibalism, resource competition between cannibals and victims, does not play as much of a role as we focus on situations of low population density and moreover assume that juveniles and adults have exclusive resources. However, in contrast to (Claessen et al. 2004) we recognise that there are additional, indirect negative effects influencing the occurrence of the life boat mechanism: any increase in density translates into a decrease in resources and hence to a slowing down of juvenile growth. Moreover, by predating conspecifics a cannibal can forage less on alternative resources,

as it has less time available to search for it. To our knowledge these indirect, negative effects, which are embodied in the condition (6.8), have not been recognised before. The condition for the occurrence of the life boat effect is hence necessarily more complicated than proposed by (Van den Bosch et al. 1988), who argued that it occurred whenever the expected energy gain from cannibalizing a single juvenile is sufficient to produce a new single offspring (see Section 4.1 of (Diekmann et al. 2003) for explicit incorporation of the subtle aspect that those juveniles that are cannibalized, but wouldn't have reached adulthood anyhow because of death of other causes, come for free). (Polis 1981) proposed that the persistence of cannibalistic populations under conditions under which non-cannibalistic populations go extinct results from that adult individuals by cannibalizing offspring indirectly gain access to a juvenile resource base, which is otherwise inaccessible to them. The condition (6.8) relates to that, since it clearly expresses that the life boat effect will only occur whenever adult resources are scarce and the adults require the indirect access to juvenile resources for persistence. Our analysis shows furthermore that cannibalism may evolve under a wider range of conditions, independent of the population level effect. However, both the onset of cannibalism and the life boat effect do depend crucially on the direct positive effect of cannibalism, the energy gain from eating a smaller conspecific, which should be contrasted with the fact that half of the previous models on cannibalism do not take this positive aspect into account, including the well-studied model of the population dynamics of Tribolium (Costantino et al. 1997).

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