INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
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SMR.780 - 15

FOURTH AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(24 October - 11 November 1994)

"Continuous Structured Population Models"

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Continuous Structured Population Models

(McKendrick, 1926; von Foerster, 1959; Frauenthal, 1986)

$\rho(t,a)$ = *population density*

t = *time*

a = *age*

$\int_{a_1}^{a_2} \rho(t,a)\,da$ = *number of individuals between ages* a_1 *and* a_2

$\beta(a)$ = *birth rate*

$\delta(a)$ = *death rate*

$\hat{\rho}(a)$ = *initial distribution*

$$\lim_{h\to 0} \frac{\rho(t+h,a+h) - \rho(t,a)}{h} + \delta(a)\,\rho(t,a) = 0$$

(conservation law)

Model

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} = -\delta(a)\,\rho$$

$$\rho(t,0) = B(t) = \int_0^\infty \beta(a)\,\rho(t,a)\,da$$

$$\rho(0,a) = \hat{\rho}(a)$$

Method of characteristics:

$$\frac{dt}{ds} = 1$$

$$\frac{da}{ds} = 1$$

$$\frac{d\rho}{ds} = -\delta(a)\,\rho(t,a)$$

$$\rho(t,a) = \begin{cases} \rho(t-a,0)\, e^{\int_0^a \delta(\alpha)\, d\alpha} & \text{if } t \geq a \\ \rho(0,a-t)\, e^{-\int_{a-t}^a \delta(\alpha)\, d\alpha} & \text{if } t < a \end{cases}$$

$$= \begin{cases} B(t-a)\, L(a) & \text{if } t \geq a \\ \hat{\rho}(a-t)\, \dfrac{L(a)}{L(a-t)} & \text{if } t < a \end{cases}$$

Sharpe-Lotka Model (1911)

$$B(t) = \int_0^\infty \beta(a)\, \rho(t,a)\, da$$

$$= \int_0^t \beta(a)\, B(t-a)\, L(a)\, da$$

$$+ \int_t^\infty \beta(a)\, \hat{\rho}(a-t)\, \frac{L(a)}{L(a-t)}\, da$$

$$= \int_0^t \beta(a)\, B(t-a)\, L(a)\, da + G(t)$$

When t > A, G(t) = 0, and

$$B(t) = Q_0\, e^{\lambda_0 t},$$

where

λ_0 is the unique real solution of the characteristic equation

$$\Delta(\lambda) = \int_0^\infty e^{-\lambda a} \beta(a)\, L(a)\, da = 1$$

$$R \equiv \Delta(0) = \int_0^\infty \beta(a)\, L(a)\, da$$

= *Net Reproduction Number*

NOTE:

$$R = 1 \Leftrightarrow \lambda_0 = 0$$
$$R > 1 \Leftrightarrow \lambda_0 > 0$$
$$R < 1 \Leftrightarrow \lambda_0 < 0$$

$$B(t) = \sum_i Q_i \, e^{\lambda_i t}$$

Find Q:

$$\int_0^\infty e^{-\lambda_0 t} G(t)\, dt$$

$$= \int_0^\infty e^{-\lambda_0 t} \left[B(t) - \int_0^t B(t-a)\, \beta(a)\, L(a)\, da\right] dt$$

$$= Q_0 \int_0^\infty \left[1 - \int_0^t e^{-\lambda_0 a} \beta(a)\, L(a)\, da\right] dt + S$$

$$= Q_0 \int_0^\infty \int_t^\infty e^{-\lambda_0 a} \beta(a)\, L(a)\, da\, dt + S$$

$$= Q_0 \int_0^\infty a\, e^{-\lambda_0 a} \beta(a)\, L(a)\, da + S$$

Show S = 0

$$Q_0 = \frac{\int_0^\infty e^{-\lambda_0 t} G(t)\, dt}{\int_0^\infty a\, e^{-\lambda_0 a} \beta(a)\, L(a)\, da}$$

Asymptotic Behavior

$$\rho(t, a) = B(t-a)\, L(a)$$

$$\sim Q_0\, e^{\lambda_0 t} e^{-\lambda_0 a} L(a)$$

$$= C(a)\, e^{\lambda_0 t}$$

C(a) is "Stable Age Distribution"

Zero Population Growth

(Frauenthal, 1986)

$$\lambda_0 = 0 \quad \textit{if and only if} \quad R = 1$$

Say population is growing (R > 1), and

$$\rho(t,a) = (Qe^{\lambda a}L(a))\,e^{\lambda t}, \qquad \lambda > 0$$

At time t=0, suppose

$$\bar{\beta}(a) = \frac{\beta(a)}{R},$$

so that

$$\bar{R} = 1.$$

Now consider

$$\lim_{t\to\infty}\bar{\rho}(t,a) \equiv \bar{\rho}_\infty(a) = \bar{Q}L(a)$$

$$\bar{Q} = \frac{\int_0^\infty \bar{G}(t)\,dt}{\int_0^\infty a\bar{\beta}(a)\,L(a)\,da}$$

$$= \frac{Q(R-1)}{\lambda\int_0^\infty a\beta(a)\,L(a)\,da}$$

$$\bar{\rho}_\infty(a) = \bar{Q}L(a)$$

$$= \frac{Q(R-1)L(a)}{\lambda\int_0^\infty a\beta(a)L(a)\,da}$$

Thus,

$$\frac{P_\infty}{P_0} = \frac{\int_0^\infty \bar{\rho}_\infty(a)\,da}{\int_0^\infty C(a)\,da}$$

$$= \frac{(R-1)\int_0^\infty L(a)\,da}{\lambda\int_0^\infty a\beta(a)L(a)\,da\int_0^\infty e^{-\lambda a}L(a)\,da}$$

Momentum of Population Growth

Song and Yu, 1988

China: R = 1.3 in 1975

$$\frac{P_\infty}{P_0} = 1.85$$

So population almost doubles before equilibrating.

Survival of the Fittest: Asymptotic Competitive Exclusion in Structured Population and Community Models

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Model: Population structured in age and q mass variables with n competing ecotypes

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} + \sum_{j=1}^{q} \frac{\partial}{\partial m_j}(\rho_i g_{ij}) = -\mu_i(t,a,\vec{m},P(t))\,\rho_i$$

$$\rho_i(t,0,\vec{m}_0) = \int_\Omega \int_0^\infty \beta_i(t,a,\vec{m},\vec{m}_0,P(t))\,\rho_i(t,a,\vec{m})\,da\,d\vec{m}$$

$$\rho_i(0,a,\vec{m}) = \hat{\rho}_i(a,\vec{m})$$

$$P(t) = F(\rho_1(t,\cdot,\cdot),\rho_2(t,\cdot,\cdot),\ldots,\rho_n(t,\cdot,\cdot))$$

t = time

a = age

$\vec{m} = (m_1, m_2, \ldots, m_q)$ = mass vector

$\rho_i(t,a,\vec{m})$ = density of i^{th} ecotype in numbers per unit age per unit mass per unit volume

$P(t)$ = any time-dependent measure of population (total numbers, total biomass, etc.)

$\frac{dm_j}{ds} = g_{ij}(t,a,\vec{m},P(t))$ = growth rate along characteristics of j^{th} mass variable in an individual organism of ecotype i

$\mu_i(t,a,\vec{m},P(t))$ = mortality rate

$\beta_i(t,a,\vec{m},\vec{m}_0,P(t))$ = birth rate

Asymptotic Competitive Exclusion

Given two ecotypes: what condition(s) guarantee

$$\lim_{t\to\infty} \frac{P_{Ti}(t)}{P_{Tj}(t)}$$

$$= \frac{\int_\Omega \int_0^\infty \rho_i(t,a,\vec{m})\, da\, d\vec{m}}{\int_\Omega \int_0^\infty \rho_j(t,a,\vec{m})\, da\, d\vec{m}} = \infty \quad ?$$

---

* We say "ecotype i dominates ecotype j"

* If total numbers are bounded, $P_{Tj}(t) \to 0$.

Age Structured Case

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} = -\mu_i(t,a,P(t))\,\rho_i$$

$$\rho_i(t,0) = \int_0^A \beta_i(t,a,P(t))\,\rho_i(t,a)\,da$$

$$\rho_i(0,a) = \hat{\rho}_i(a)$$

$$P(t) = F(\rho_1(t,\cdot),\rho_2(t,\cdot),\ldots,\rho_n(t,\cdot))$$

Method of characteristics for systems of quasi-linear PDE's with same principle part (Courant and Hilbert, 1962)

$$\frac{dt}{ds} = 1$$

$$\frac{da}{ds} = 1$$

$$\frac{d\rho_i}{ds} = -\mu_i(t,a,P(t))\,\rho_i(t,a)$$

Survivorship:

$$\rho_i(t,a) = \begin{cases} \rho_i(t-a,0)\, L_i(t,a,P) & \text{if } t \geq a \\ \rho_i(0,a-t)\, M_i(t,a,P) & \text{if } t < a \end{cases}$$

where

$$L_i(t,a,P) = e^{-\int_0^a \mu_i(t-a+\alpha,\alpha,P(t-a+\alpha))\,d\alpha} =$$

probability of survival until age a for organisms born at time t-a

$$M_i(t,a,P) = e^{-\int_{a-t}^a \mu_i(t-a+\alpha,\alpha,P(t-a+\alpha))\,d\alpha} =$$

probability of survival until age a given survival at age a-t and time 0

Classification of Results

Conditions which guarantee ρ_1 dominates ρ_2

Case 1: $\beta_i = \beta_i(a)$ *and* $\mu_i = \mu_i(a)$

$$\forall a \in [0,A]\ (\beta_1(a)\, L_1(a) \geq \beta_2(a)\, L_2(a))$$

with strict inequality holding at least once

Case 2: $\beta_i = \beta_i(a)$, $\mu_i = \sigma_i(a) + \nu(t,P(t))$

$$\forall a \in [0,A]$$
$$\forall t \in [0,\infty)\ (\beta_1(a)\, L_1(t,a,P) \geq \beta_2(a)\, L_2(t,a,P))$$

iff

$$\forall a \in [0,A]\ (\beta_1(a)\, e^{-\int_0^a \sigma_1(\alpha)\,d\alpha} \geq \beta_2(a)\, e^{-\int_0^a \sigma_2(\alpha)\,d\alpha})$$

with strict inequality holding at least once

Case 3:

$\beta_i = \beta_i(a)$, *and* $\mu_i = \mu_i(t,a)$; *or*
$\beta_i = \beta_i(t,a,P(t))$ *and* $\mu_i = \mu_i(a)$

$\exists k > 1 \ni$

1)
$\forall a \in [0,A]$
$\forall t \in [a,\infty) \; (\beta_1(a) L_1(t,a) \geq k^a \beta_2(a) L_2(t,a))$

2)
$\forall a \in [0,A]$
$\forall \alpha \in [0,a] \; (\hat{\rho}_1(a-\alpha)\beta_1(a) M_1(\alpha,a)$

$\geq k^{\alpha} \hat{\rho}_2(a-\alpha)\beta_2(a) M_2(\alpha,a))$

3)
$\hat{\rho}_1(0) > \hat{\rho}_2(0)$

Case 4:
$\beta_i = \beta_i(t,a,P(t))$, *and* $\mu_i = \mu_i(t,a,P(t))$

$\exists k > 1 \ni$

1) $\forall a \in [0,A]$
$\forall t,p \in [0,\infty) \; (\beta_1(t,a,p) \geq k^a \beta_2(t,a,p))$

2) $\forall a \in [0,A]$
$\forall t,p \in [0,\infty) \; (\mu_1(t,a,p) \leq \mu_2(t,a,p))$

3)
$\forall a \in [0,A] \; \forall \alpha \in [0,a]$

$\hat{\rho}_1(a-\alpha) \geq k^{\alpha-a} \hat{\rho}_2(a-\alpha)$

with strict inequality holding at $a=\alpha$

Note: 1-3 are used to establish the sufficient conditions

$$\beta_1(t,a,P(t)) L_1(t,a,P) \geq$$

$$k^a \beta_2(t,a,P(t)) L_2(t,a,P), \quad etc.$$

Theorem (Induction on Closed, Bounded-Below Subsets of $\mathbb{R}$)

(Henson and Hallam, 1994)

Let Q be a proposition and "$Q(t)$" mean "$Q(t)$ is true." Suppose that $K \subset \mathbb{R}$ is closed and bounded below, and that

1) The truth set $A = \{t \in \mathbb{R} \mid Q(t)\}$ is open in $\mathbb{R}$; and
2) for all $t \in K$, we have $Q(t)$ whenever $Q(x)$ for all $x \in K$ such that $x < t$.

Then

$$\forall t \in K(Q(t)).$$

Proof Let "$\sim Q(t)$" mean "not $Q(t)$". Suppose for some $t \in K$, $\sim Q(t)$. Then $(\mathbb{R}-A) \cap K$ is nonempty, closed, and bounded below, and so contains its infimum T. Thus, $\sim Q(T)$, which contradicts hypothesis 2. ■

Theorem Let $\beta_i = \beta_i(t, a, P(t))$ *and* $\mu_i = \mu_i(a)$ (Case 3). If there exists a $k > 1$ such that

1)
$\forall a \in [0, A]\ \forall t \in [a, \infty)\ \forall p \in [0, \infty)$

$$\beta_1(t, a, p)\, L_1(a) \geq k^a \beta_2(t, a, p)\, L_2(a)$$

2)
$\forall a \in [0, A]\ \forall \alpha \in [0, a]\ \forall p \in [0, \infty)$

$$\hat{\rho}_1(a-\alpha)\, \beta_1(\alpha, a, p)\, M_1(a) \geq$$

$$k^\alpha \hat{\rho}_2(a-\alpha)\, \beta_2(\alpha, a, p)\, M_2(a)$$

3)
$\hat{\rho}_1(0) > \hat{\rho}_2(0)$,

then ρ_1 dominates ρ_2.

Proof Continuously extend $\rho_1(t,0)$ and $\rho_2(t,0)$ to all of $\mathbb{R}$ by defining $\rho_i(t,0) = \rho_i(0,0)$ for $t < 0$. Then the truth set $\{t\in\mathbb{R} \mid \rho_1(t,0) > k^t\rho_2(t,0)\}$ is open in $\mathbb{R}$. Let $T\in[0,\infty)$. If $T = 0$, then $\rho_1(T,0) > k^T\rho_2(T,0)$ by hypothesis 3.

Otherwise, assume $\rho_1(t,0) > k^t\rho_2(t,0)$ for all $t\in[0,T)$. We will show that $\rho_1(T,0) > k^T\rho_2(T,0)$, and then apply the induction theorem.

$$\begin{aligned}
&\rho_1(T,0)\\
&= \int_0^A \beta_1(T,a,P(T))\,\rho_1(T,a)\,da\\
&= \int_0^T \beta_1(T,a,P(T))\,\rho_1(T-a,0)\,L_1(a)\,da\\
&+ \int_T^A \beta_1(T,a,P(T))\,\hat{\rho}_1(a-T)\,M_1(a)\,da\\
&> \int_0^T \beta_2(T,a,P(T))\,k^{T-a}\rho_2(T-a,0)\,k^a L_2(a)\,da\\
&+ \int_T^A \beta_2(T,a,P(T))\,k^T\hat{\rho}_2(a-T)\,M_2(a)\,da\\
&= k^T\int_0^T \beta_2(T,a,P(T))\,\rho_2(T,a)\,da\\
&+ k^T\int_T^A \beta_2(T,a,P(T))\,\rho_2(T,a)\,da\\
&= k^T\rho_2(T,0).
\end{aligned}$$

Thus, $\rho_1(t,0) > k^t\rho_2(t,0)$ for all $t\in[0,\infty)$; and for each $a\in[0,A]$,

$$\begin{aligned}
\lim_{t\to\infty}\frac{\rho_1(t,a)}{\rho_2(t,a)} &= \lim_{t\to\infty}\frac{\rho_1(t-a,0)\,L_1(a)}{\rho_2(t-a,0)\,L_2(a)}\\
&\geq \lim_{t\to\infty} k^{t-a}\frac{L_1(a)}{L_2(a)}\\
&= \infty.
\end{aligned}$$

This limit is uniform in a, and hence

$$\lim_{t\to\infty}\frac{P_{T1}(t)}{P_{T2}(t)} = \lim_{t\to\infty}\frac{\int_0^A \rho_1(t,a)\,da}{\int_0^A \rho_2(t,a)\,da} = \infty. \qquad \blacksquare$$

Age-Size Structured Model

$$\ldots_i + \frac{\partial \rho_i}{\partial a} + \frac{\partial}{\partial m}(\rho_i g_i) = -\mu_i(t,a,m,P(t))\rho_i$$

$$\ldots t,0,m_0) = \int_0^M \int_0^A \beta_i(t,a,m,m_0,P(t))\,\rho_i(t,a,m)\,da\,dm \quad (1)$$

$$\ldots 0,a,m) = \hat{\rho}_i(a,m)$$

$$\ldots) = F(\rho_1(t,\cdot,\cdot),\rho_2(t,\cdot,\cdot),\ldots,\rho_n(t,\cdot,\cdot)).$$

…blem: Ecotype models do not have same principle …. To compare ecotypes 1 and 2, structure both in … and m_2.

$$\ldots_i + \frac{\partial \rho_i}{\partial a} + \frac{\partial}{\partial m_1}(\rho_i g_1) + \frac{\partial}{\partial m_2}(\rho_i g_2) \quad \mu_i(t,a,m_1,P(t))\rho_i$$

$$\ldots t,0,m_{10},m_{20}) = \int_0^M \int_0^M \int_0^A \tilde{\beta}_i(t,a,m_i,m_{10},m_{20},P(t))\,\rho_i(t,a,m_1,m_2)\,da\,dm_1\,dm_2 \quad (2)$$

$$\ldots 0,a,m_1,m_2) = \hat{\rho}_i(a,m_1,m_2)$$

$$\ldots) = \overline{F}(\rho_1(t,\cdot,\cdot,\cdot),\ldots,\rho_n(t,\cdot,\cdot,\cdot)),$$

Model (2) can be reduced to model (1):

$q_i(t,a,m_i) = \int_0^M \rho_i(t,a,m_1,m_2)\,dm_j,\ j \neq i$, is the solution to Equation (1) under the **assumptions**

1. $\hat{q}_i(a,m_i) = \int_0^M \hat{\rho}_i(a,m_1,m_2)\,dm_j, \quad i \neq j;$

2. $g_j = 0$ whenever $m_j = M$ or $m_j = 0$;

3. $F(\int_0^M \rho_1(t,\cdot,\cdot,m_2)\,dm_2, \int_0^M \rho_2(t,\cdot,m_1,\cdot)\,dm_1) = \overline{F}(\rho_1(t,\cdot,\cdot,\cdot),\rho_2(t,\cdot,\cdot,\cdot))$; and

4. $\tilde{\beta}_i = \beta_i(t,a,m_i,m_{i0},P(t))\,D_i(m_{j0}),\ i \neq j$, with $\int_0^M D_i(m_{j0})\,dm_{j0} = 1$.

Each equation now has same principle part:

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial \rho_i}{\partial a} + g_1\frac{\partial \rho_i}{\partial m_1} + g_2\frac{\partial \rho_i}{\partial m_2} = -(\mu_i + \frac{\partial g_1}{\partial m_1} + \frac{\partial g_2}{\partial m_2})\rho$$

CONCLUSIONS

* βL is a good measure of ecotypic fitness

* density and time dependence in mortality that uniformly affects the different morphs does not modify characteristic behavior

Intraspecific Competition:

Scramble vs Contest

(Lominicki, 1984)

Scramble Competition: Each individual in the population can alter the resource consumption of every other individual.

Contest Competition: Resource intake of an individual cannot be altered by younger individuals but can be altered by older individuals.

Lomnicki: Contest competition is more "resilient" or "stable" than scramble competition.

(Cushing, 1994)

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} = -\delta \rho$$

$$\rho(t,0) = \int_0^\infty \beta \rho(t,a)\, da$$

$$\rho(0,a) = \hat{\rho}(a)$$

where

$$\beta = \beta(t, Y(t,a), \Theta(t,a))$$

$$\delta = \delta(t, Y(t,a), \Theta(t,a))$$

and

$$Y(t,a) = \int_0^a \rho(t,\alpha)\, d\alpha$$

$$\Theta(t,a) = \int_a^\infty \rho(t,\alpha)\, d\alpha$$

$$P(t) = Y + \Theta$$

NOTE: $dY = \rho(t,a)\, da$

Total Population Birth and Death Rates

$$B(t,P) = \int_0^\infty \beta(t, Y, \Theta)\, \rho(t,a)\, da$$

$$= \int_0^P \beta(t, u, P-u)\, du$$

$$D(t,P) = \int_0^\infty \delta(t, Y, \Theta)\, \rho(t,a)\, da$$

$$= \int_0^P \delta(t, u, P-u)\, du$$

$$P' = B(t,P) - D(t,P)$$

$$P(0) = \int_0^\infty \hat{\rho}(a)\, da$$

(Cushing and Henson, 1994, in progress)

Assume:

$\beta = \beta_0 u(Rc)$

$\delta = \delta_0$

u = *resource uptake rate*

R = *resource available to individual in absence of competition*

Rc = *resource available to individual of age a in presence of competition*

Scramble: $c_s = c_s(P(t))$

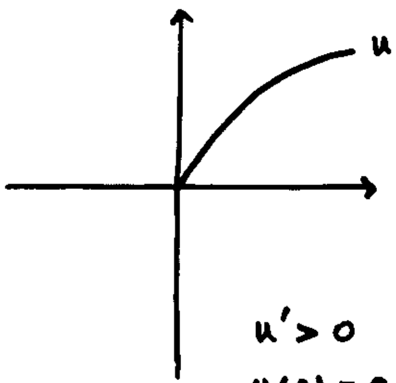
Contest: $c_c = c_c(\Theta(t,a))$

Comparison Criterion ("Same amount" of competition):

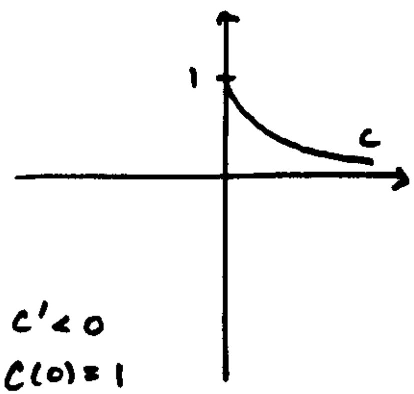
Define

$$c_s(P) \equiv \frac{1}{P}\int_0^P c_c(z)\,dz$$

Assume



$u' > 0$
$u(0) = 0$



$c' < 0$
$c(0) = 1$
$c(\infty) = 0$
$\int_0^\infty c(z)\,dz \le 1$

Let

$$n = \frac{\beta_0 u(R)}{\delta_0}$$

Scramble:

$$P' = \beta_0 u\left(R\frac{1}{P}\int_0^P c(z)\,dz\right) P - \delta_0 P$$

$$= \delta_0 P \left[n \frac{u\left(R\frac{1}{P}\int_0^P c(z)\,dz\right)}{u(R)} - 1\right]$$

Contest:

$$P' = \beta_0 \int_0^P u(Rc(z))\,dz - \delta_0 P$$

$$= \delta_0 P \left[n \frac{1}{p}\int_0^P \frac{u(Rc(z))}{u(R)}\,dz - 1\right]$$

Existence and Global Stability of Equilibria

1. $n < 1 \Rightarrow P \to 0$ *as* $t \to \infty$
2. $n > 1 \Rightarrow P = 0$ *is unstable* *and* $\exists!\, P_\infty > 0$
3. P_∞ *is globally stable.*

Jensen's Inequality implies

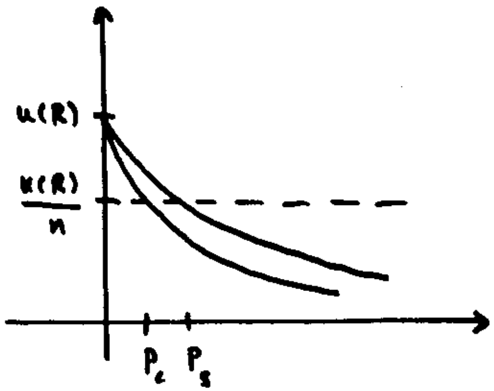
$$u'' < 0 \Rightarrow \forall P > 0$$

$$u\left(R\frac{1}{P}\int_0^P c(z)\,dz\right) > \frac{1}{P}\int_0^P u(Rc(z))\,dz$$

At equilibrium,

$$u\left(R\frac{1}{P_s}\int_0^{P_s} c(z)\,dz\right) = \frac{u(R)}{n}$$

$$= \frac{1}{P_c}\int_0^{P_c} u(Rc(z))\,dz$$



$$u'' < 0 \Rightarrow P_s > P_c$$

$$u'' > 0 \Rightarrow P_s < P_c$$

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