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QUALITATIVE ANALYSIS OF OSCILLATIONS IN ISOLATED POPULATIONS OF FLIES

by

J.F.Perez, C.P.Malta and F.A.B. Coutinho
Instituto de Física - Universidade de São Paulo

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SUMARY

Populations oscillations in isolated populations of flies are considered. Qualitative methods of analysis are applied to the functional difenrential equation representing the system and conditions for the occurence of oscillations are derived. These conditions are readily vizualized in terms of parameters which are easily measured and have a straightforward biological interpretation.

Running Headline:

Oscillations in Isolated Populations of Flies.

1. INTRODUCTION

Oscillations in isolated populations of the blowfly Lucilia were first observed by Nicholson (1954). Recently, analogous oscillations in populations of Drosophyla Sturtevan tis were observed by Mourão and Tadei (1974) and to our knowledge a mathematical analysis of this phenomena was given only by Maynard-Smith (1968,1974) (see also Goel, Samaresch & Montroll 1971). In both publications by Maynard-Smith the oscillations were atributed to the time interval τ required for an egg to become an adult fly.

However the equation proposed by Maynard-Smith to describe the phenomena in his first publication is different from the one proposed more recently. The equation proposed in the first publication is a non linear differential difference equation and is analysed only numerically. The equation proposed in the second publication is a linear differential difference equation and is analysed by means of Laplace transform techniques. This second equation has a "driving term" and therefore has the serious drawback of not having a zero population as an unstable solution and furthermore has unbounded oscillating solutions.

The content of this paper is as follows. In the section II we propose a somewhat modified form of the equation proposed in Maynard-Smith (1968). The chief advantage of our formulation is that it depends on parameters that have a transparent physical interpretation and furthermore are easily measurable. We also show that the equation proposed in Maynard-Smith (1974) results from an inappropriate expansion of our equation. Then in section III we analyse the solutions of this modified equation in terms of the parameters range and give several sufficient conditions for the oscillations to occur.

In section IV we present the results of numerical integration of our equation for several cases suggested by the analysis made in section III. It is shown that our equation admits solution with very peculiar oscillatory behaviour which to our knowlwdge has not been so far detected. It is also discussed the conditions for experimentally detecting this behaviour.

II. THE EQUATION

The populations studied in Nicholson (1954) and Mourão and Tadei (1974) were fly populations confined to live in cages, and receiving a fixed limited amount of food. Let N_t be the number of flies per unit volume of the cage at the time t. The habitat (that is the cages) can be characterized by two functions of N_t:$b(N_t)$ the birth rate per head and $\lambda(N_t)$ the death rate per head.

Qualitatively, the general form of these two functions is as shown in Fig. 1 that is, $\lambda(N_t)$ is a monotonicaly increasing function of N_t and $b(N_t)$ is a monotonicaly decreasing function of N_t satisfying the conditions: $\lambda(0)<b(0)$, $b(\infty)=0$ and $\lambda(\infty)=\infty$.

Unless explicitly stated $\lambda(N_t)$ and $b(N_t)$ are assumed to be infinitely differentiable.

FIGURE 1

Let τ be the time interval which is required for an egg to become an adult fly.

Then we have

$$\frac{dN_t}{dt} = b(N_{t-\tau})\ N_{t-\tau} - \lambda(N_t)\ N_t \qquad (1)$$

The first equation proposed by Maynard-Smith (1968) can be obtained from equation (1) by replacing $b(N_t)$ by $(a-bN_t)$ and assuming $\lambda(N_t)$ to be a constant. We shall see in the next sections that it is not necessary to make such drastic simplifications to analyse equation (1).

The second equation proposed by Maynard-Smith (1974) follows from atributing the decrease in birth rate with N_t to lack of food. His reasoning is the following: lét ω be the amount of food per unit volume supplied per unit time to the flies. Then the amount available per unit time for each adult is ω/N_t. Assuming that each adult consumes a fixed amount ξ just to survive without laying any egg then the excess food available for eggs productions is $G=\omega/N_t - \xi$. At this stage Maynard-Smith (1974) assumes that the birth rate $b(N_t)$ is proportional to G, that is, $b(N_t) = kG$. The driving term in his equation results from the fact that $G \rightarrow \infty$ as $N_t \rightarrow 0$. Note however that what can really be said is that the birth rate is a function $\Phi(G)$ with the following shape (fig.2).

FIGURE 2

We should then write

$$\frac{dN_t}{dt} = \Phi\left(\frac{\omega}{N_{t-\tau}} - \xi \right) N_{t-\tau} - \lambda(N_t)\, N_t$$

and a new function $b(N_t)$ can be defined such that $b(N_t) = \Phi(\omega/N_t - \xi)$ so that equation (1) is recovered.

Let's call $\bar{N}$ the equilibrium density which is the value of the population density corresponding to the intersection of the curves $\lambda(N_t)$ and $b(N_t)$ (see fig. 1).

We can then rewrite equation (1) in terms of a new variable $\delta N_t = N_t - \bar{N}$

$$\frac{d\delta N_t}{dt} = b(\bar{N}+\delta N_{t-\tau})\ (\delta N_{t-\tau}+\bar{N})-\lambda(\bar{N}+\delta N_t)\ (\delta N_t+\bar{N}) \tag{2}$$

Let's now expand

$$b(\bar{N}+\delta N_t)=b(\bar{N})+\delta N_t\left(\frac{db}{dN_t}\right)_{\bar{N}}+R_b(\delta N_t) \tag{3}$$

and

$$\lambda(\bar{N}+\delta N_t)=\lambda(\bar{N})+\delta N_t\left(\frac{d\lambda}{dN_t}\right)_{\bar{N}}+R_\lambda(\delta N_t) \tag{4}$$

where $R_b(\delta N_t)$ and $R_\lambda\ (\delta N_t)$ go to zero at least as $(\delta N_t)^2$ as δN_t goes to zero.

Substituting (3) and (4) in (2) we have

$$\frac{d\delta N_t}{dt}-\left[b(\bar{N})+\bar{N}\left(\frac{db}{dN_t}\right)_{\bar{N}}\right]\delta N_{t-\tau}+\left[\lambda(\bar{N})+\bar{N}\left(\frac{d\lambda}{dN_t}\right)_{\bar{N}}\right]\delta N_t =$$

$$=\left(\frac{db}{dN_t}\right)_{\bar{N}}(\delta N_{t-\tau})^2-\left(\frac{d\lambda}{dN_t}\right)_{\bar{N}}(\delta N_t)^2+R_b(\delta N_{t-\tau})(\bar{N}+\delta N_{t-\tau})-R_\lambda(\delta N_t)(\bar{N}+\delta N_t) \tag{5}$$

In the next section we shall show that the existence of oscillatory solutions around the equilibrium value $N_t=\bar{N}$ for equation (5) depends only on the relative value of the parameters,

$$\eta=b(\bar{N})=\lambda(\bar{N})\quad;\quad\left(\frac{db}{dN_t}\right)_{\bar{N}}\quad;\quad\left(\frac{d\lambda}{dN_t}\right)_{\bar{N}}\qquad\text{and}\quad\tau$$

which represent the birth (or death) rate at equilibrium, the slopes of the birth rate curve and the death rate curve respectively at the equilibrium density and the time time interval required for an egg to become an adult fly.

III. SUFFICIENT CONDITIONS FOR STABILITY OF THE EQUILIBRIUM SOLUTION $N_t=\bar{N}$

In this section we shall obtain sufficient conditions for stability of the equilibrium solution $N_t=\bar{N}$. Violation of these sufficient conditions will give necessary conditions for the existence of unstable solutions of oscillatory type.

Let's in equation (5) call

$$B = \eta+\bar{N}\left(\frac{db}{dN_t}\right)_{\bar{N}} \tag{6}$$

and

$$\Lambda=\eta+\bar{N}\left(\frac{d\lambda}{dN_t}\right)_{\bar{N}} \tag{7}$$

By the assumptions on b and λ (Fig.1) $\left(\frac{db}{dN_t}\right)_{\bar{N}} \leq 0$ and $\left(\frac{d\lambda}{dN_t}\right)_{\bar{N}} \geq 0$, so that in general $B < \Lambda$. Note that B can be negative.

Equation (5) has $\delta N_t=0$ as a solution and this solution is asymptoticaly stable (El'sgol'ts 1966) if all the roots of the following equation (Bellman and Cooke - 1963)

$$S-\Lambda-B\ e^{-\tau S} =0 \tag{8}$$

have negative real part. On the other hand, if equation (8) has at least one solution with positive real part then $\delta N_t=0$ is an unstable solution (El'sgol'ts 1966) of equation (5) and therefore equation (5) admits oscillatory solution.

If $S_L=S_1+iS_2$ is a solution of equation (8) so is S_L^* and therefore we should speak of a pair of roots. Rewriting equation (8) in terms of S_1 and S_2 we have

$$S_1 + \Lambda = B\, e^{-\tau S_1} \cos\tau S_2 \tag{9}$$

$$S_2 = -B\, e^{-\tau S_1} \sin\tau S_2 \tag{10}$$

or

$$(S_1+\Lambda)^2 + S_2^2 = B^2\, e^{-2\tau S_1} \tag{11}$$

for a fixed S_2 we have an oscillatory solution if the intersection of the two curves, $f_1(S_1) = (S_1+\Lambda)^2 + S_2^2$ and $f_2(S_1) = B^2\, e^{-2\tau S_1}$, occurs to the right of the origin.

The curves $f_1(S_1)$ and $f_2(S_1)$ are plotted in Fig. (3)

FIGURE 3

So we see that there is no oscillation if

$$B^2 \leqslant S_2^2 + \Lambda^2 \tag{12}$$

or surely if

$$B^2 \leqslant \Lambda^2 \qquad \text{or} \qquad -\Lambda \leqslant B \leqslant \Lambda \tag{13}$$

Using equations (6) and (7) we obtain:

$$-\left[\eta + \bar{N}\left(\frac{d\lambda}{dN_t}\right)_{\bar{N}}\right] \leqslant \left[\eta + \bar{N}\left(\frac{db}{dN_t}\right)_{\bar{N}}\right] \leqslant \left[\eta + \bar{N}\left(\frac{d\lambda}{dN_t}\right)_{\bar{N}}\right]$$

$$\left(\frac{db}{dN_t}\right)_{\bar{N}} \leqslant \left(\frac{d\lambda}{dN_t}\right)_{\bar{N}} \tag{14}$$

and

$$\left(\frac{db}{dN_t}\right)_{\bar{N}} \geqslant -\left[\frac{2\eta}{\bar{N}} + \left(\frac{d\lambda}{dN_t}\right)_{\bar{N}}\right] \tag{15}$$

A better sufficient condition can be obtained from equations (6) and (7). In order to have an oscillatory solution S_1 must be positive and we can see from equation (9) that this condition can be satisfied only if $\cos \tau S_2$ is negative because if $\cos \tau S_2 > 0$, equation (9) gives:

$$S_1 + \Lambda = B\, e^{-\tau S_1} \cos \tau S_2 < B$$

or

$$S_1 < B - \Lambda$$

or

$$S_1 < \bar{N}\left[\left(\frac{db}{dN_t}\right)_{\bar{N}} - \left(\frac{d\lambda}{dN_t}\right)_{\bar{N}}\right] < 0$$

Therefore cos τS_2 must be negative and a necessary condition for oscillation to occur is

$$2n\pi + \frac{\pi}{2} \leq |\tau S_2| \leq \pi + 2n\pi \qquad (16)$$

and equation (12) gives

$$B^2 \leq \left(\frac{\pi}{2\tau}\right)^2 + \Lambda^2 \qquad (17)$$

as a sufficient condition for no oscillation. Therefore, violation of (17) is a necessary condition for oscillation to occur. Note that if τ is very small condition (16) is always satisfied and no oscillation can occur.

Let's now give sufficient conditions for the existence of 2n pairs of roots with positive real part. To this end let's investigate the behaviour of a root as a function of τ. The pair of equations:

$$S_1(\tau) + \Lambda = B\, e^{-\tau S_1(\tau)} \cos \tau S_2(\tau) \qquad (18)$$

$$S_2(\tau) = -B\, e^{-\tau S_1(\tau)} \sin \tau S_2(\tau) \qquad (19)$$

define implicitly the functions $S_1(\tau)$ and $S_2(\tau)$.

For B and Λ satisfying equation (13), equation (16) shows that for small values of τ all roots of equation (8) have $S_1 < 0$. Increasing τ we can see that there exists a $\tau = \tau_1$, for which a pair of solutions reaches the imaginary axis. In fact, equations (18) and (19) admit a solution $S_1(\tau_1)=0$ and $S_2(\tau_1)$ which is given by the solutions of

$$\Lambda = B \cos\tau_1 S_2(\tau_1) \tag{20}$$

$$S_2(\tau_1) = -B \sin \tau_1 S_2(\tau_1) \tag{21}$$

The solutions of (20) and (21) are:

$$S_2 = \pm \sqrt{B^2-\Lambda^2} = \pm\gamma \tag{22}$$

with τ_1 satisfying

$$\gamma = -B \sin \tau\gamma \tag{23}$$

$$\Lambda = B \cos \tau\gamma \tag{24}$$

Note that (22) makes sense only if the condition (13) is violated.

To solve the system of equation (23) and (24) we first note that (for $B < 0$ and $\Lambda > 0$)

$$2n\pi + \frac{\pi}{2} < \tau\gamma < 2n\pi + \pi \tag{25}$$

since we must have $\cos \tau\gamma < 0$ and $\sin \tau\gamma > 0$.

Now inspection of fig. 4 shows

FIGURE 4

that we have a set of solutions given by

$$\tau_n = \frac{1}{\gamma}\left(\theta + 2\pi(n-1)\right) \tag{26}$$

where

$$\theta = \text{arc sin}\left(- \frac{\gamma}{B}\right) \tag{27}$$

restricted to the interval $\frac{\pi}{2} < \theta < \pi$.

The value $\tau_1 = \theta/\gamma$ is the minimum value of θ such that equation (8) has a pair of roots with S_1 greater than zero. To show this we must show that the slope of the function $S_1(\tau)$ at the point $\tau = \tau_1$, is positive so that it crosses the axis.

By taking derivative of eq. 19 we obtain a linear system of equations

$$\left[1+\tau(S_1+\Lambda)\right]\frac{dS_1}{d\tau} - S_2\tau\frac{dS_2}{d\tau} = S_2^2 - (S_1+\Lambda)\, S_1 \tag{28}$$

$$\tau S_2 \frac{dS_1}{d\tau} + \left[1+\tau(S_1+\Lambda)\right]\frac{dS_2}{d\tau} = -S_2(S_1+\Lambda) - S_1 S_2 \tag{29}$$

For which the determinant

$$\Delta = \left[1+ \tau(S_1+\Lambda)\right]^2 + (\tau S_2)^2$$

is always positive, regardless of τ. In particular for a value τ_n when a pair of roots is on the imaginary axis we have

$$S_1 = 0 \quad , \quad S_2 = \pm\gamma$$

$$\Delta = (1+ \tau_n\Lambda)^2 + (\tau_n\gamma)^2 \tag{30}$$

On the other hand the determinant in the numerator of Cramer's rule for $\frac{dS_1}{d\tau}$ is

$$\Delta_1 = S_2^2 - S_1\left[(S_1+\Lambda) + \tau(S_2^2 + (S_1+\Lambda)^2)\right]$$

So that

$$\Delta_1(\tau_n) = S_2^2 = \gamma^2$$

and therefore

$$\left(\frac{dS_1}{d\tau}\right)_{\tau_n} = \frac{\gamma^2}{(1+\tau_n\Lambda)^2 + (\tau_n\gamma)^2} > 0 \qquad (31)$$

It should be noted that equation (31) is showing not only that for $\tau=\tau_n$ a pair of roots will cross the imaginary axis but also that a pair of roots crosses the imaginary axis a single time.

Before closing this section we would like to stress that conditions given by equation (13) (or (17)) are very easialy visualized, that is, it is possible to tell whether a population oscillates or not just by inspection of the curves $b(N_t)$ and $\lambda(N_t)$.

IV - NUMERICAL RESULTS

Equation (1) was solved numerically assuming for $b(N_t)$ and $\lambda(N_t)$ the following form

$$b(N_t) = \begin{cases} b_o - b_1 N_t & \text{for } N_t < N_{max} \\ 0 & \text{for } N_t > N_{max} \end{cases} \qquad (32)$$

and

$$\lambda(N_t) = \text{constant} = \eta \tag{33}$$

where

$$N_{max} = + \frac{b_o}{b_1}$$

The following results were obtained:

(i) If the condition (17) is satisfied, the solution N_t will always tend to the equilibrium solution $\bar{N}$, independent of the initial conditions. This result suggests that if condition (17) is satisfied then $N_t = \bar{N}$ is more than a stable solution it is a solution which is stable in the large.

(ii) If condition (17) is not satisfied then oscillatory solutions were obtained independent of the initial conditions. This result suggests that if condition (17) is violated then there is no solution of equation (1) that tends to $\bar{N}$ as $t \rightarrow \infty$. This is much stronger than stating that N is an unstable solution because instability only guarantees that there exist solutions of equation (1) which do not converge to $\bar{N}$ as $t \rightarrow \infty$.

(iii) In Fig. 5 we present the qualitative behaviour of the solution of equation (1) when condition (17) is violated. Fig. 5a shows the behaviour of the solution for a set of parameters such that eq.(8) has only one root with positive real part and Fig. 5b shows the same thing for a set of parameters such that eq.(8) has 2 roots with positive real part.

The qualitative behaviour shown in Fig. 5b provides us a way of testing equation (1). According to equation (26), such a behaviour is expected if

$$\gamma\tau - \theta > 2\pi \tag{34}$$

and this condition can be fulfilled by increasing the absolute value of B and/or decreasing Λ (see equations(22) and (27)).

In one of the populations studied by Mourão and Tadei (1974) a behaviour similar to the one depicted in Fig.5b was observed. However this behaviour was observed for 2 big cycles only disappearing afterwards. Therefore we conclude that this might have happened because by pure accident equation (34) was satisfied for a certain period of time only and no special care was taken to ensure this permanently.

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FIGURE CAPTIONS

Fig. 1 - Birth rate per $b(N_t)$ and death rate per head $\lambda(N_t)$ as functions of the population density N_t. The point $\bar{N}$ is the equilibrium density and η is the value of $b(N_t)$ or $\lambda(N_t)$ at $\bar{N}$.

Fig. 2 - Birth rate per head $\Phi(G)$ as a function of $G=\omega/N_t - \xi$ which is the excess food available for egg production.

Fig. 3 - The solid curves are the function $f(S_1) = (S_1+\Lambda)^2 + S_2^2$ plotted against S_1 for three values of S_2 and the dash and dot curve is the function $f_2(S_1) = B^2 e^{-2\tau S_1}$ plotted against S_1.

Fig. 4 - This figure illustrates the graphical solution of equations (23) and (24). For given values of Λ and B, if $\tau_n < \tau < \tau_{n+1}$ equation (8) has n roots with positive real past.

Fig. 5 - Numerical solution of equation (1) with $b(N_t)$ and $\lambda(N_t)$ given by equations (32) and (33) respectively for $b_0=4.0$, $b_1 = 0.001$, $\eta = 1.0$ and two different values of τ: Figure (a) shows the solution for $\tau= 2.0$ in which case eq. (8) has only one root with positive real past since $\tau_1 = 1.2$ and $\tau_2= 4.8$.

Figure (b) shows the solution for $\tau= 5.0$ and as $\tau_3 = 8.4$ it corresponds to a case of 2 roots with positive real past.

In both figures the time scale is given by the respective value of τ.

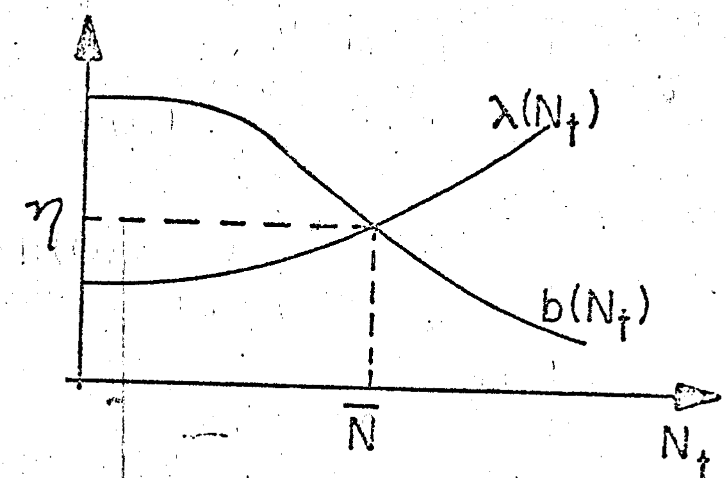


Fig. 1

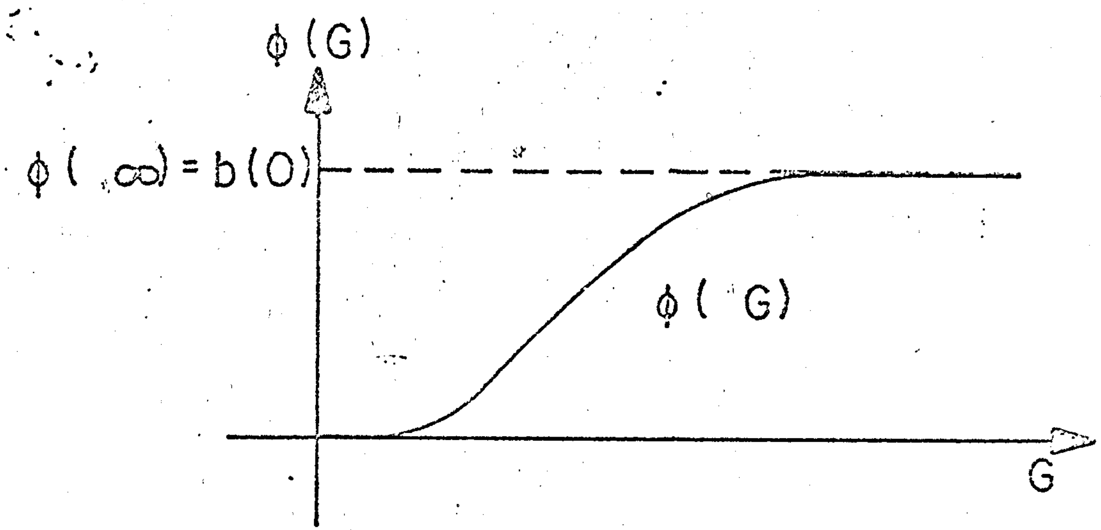


Fig. 2

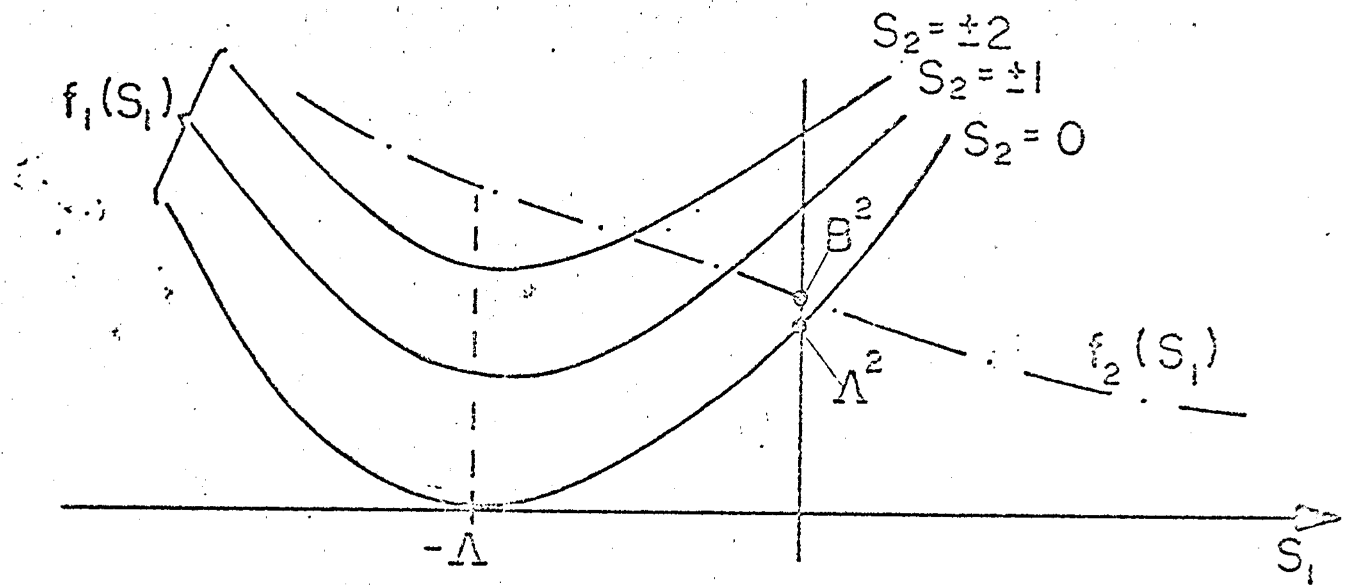


Fig. 3

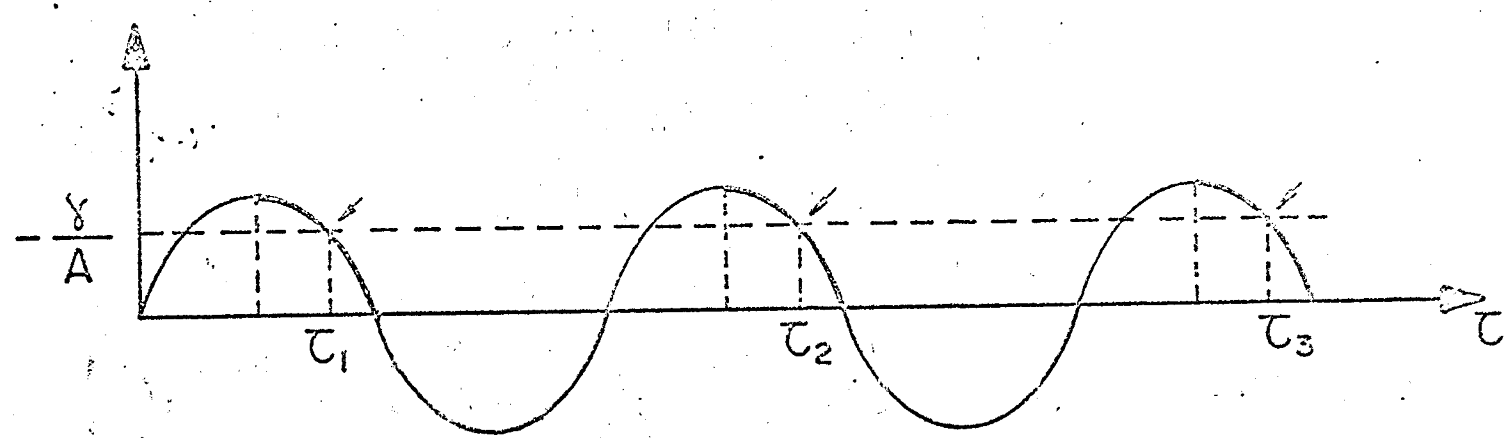


Fig.4

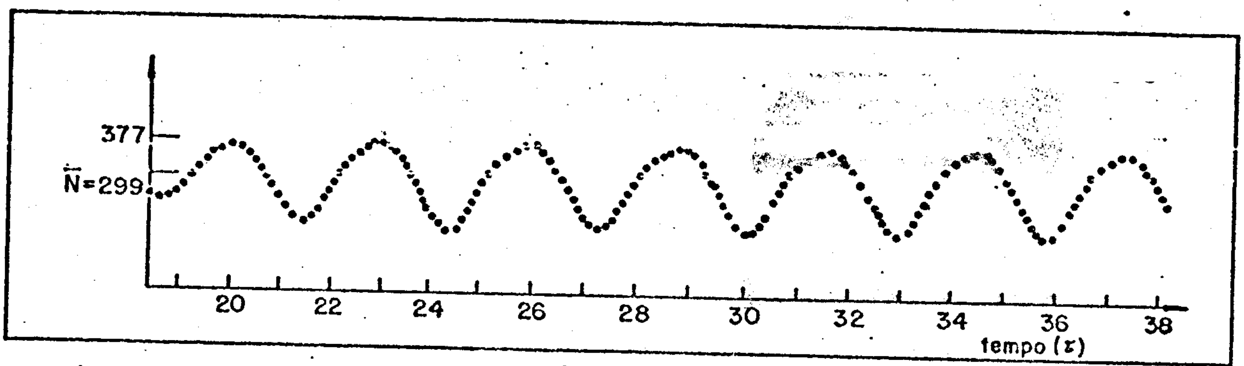
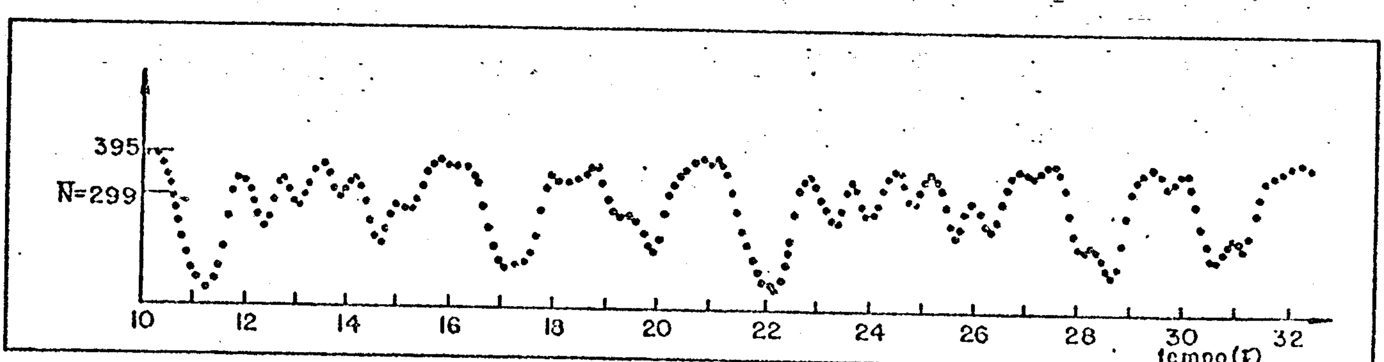

377
N̄=299
20
22
24
26
28
30
32
34
36
38
tempo (τ)

fig. 5a


395
N̄=299
10
12
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32
tempo (τ)

fig. 5b