EXERCISES

Find the bifurcation points of each of the following systems of equations.

1. $\dot{x} = \begin{pmatrix} 1 & \varepsilon \\ \varepsilon & 1 \end{pmatrix} x$

2. $\dot{x} = \begin{pmatrix} 1 & 1 \\ \varepsilon & 1 \end{pmatrix} x$

3. $\dot{x} = \begin{pmatrix} 0 & 2 \\ -2 & \varepsilon \end{pmatrix} x$

4. $\dot{x} = \begin{pmatrix} 0 & 2 \\ 2 & \varepsilon \end{pmatrix} x$

5. $\dot{x} = \begin{pmatrix} 0 & -\varepsilon \\ \varepsilon & 0 \end{pmatrix} x$

In each of Problems 6–8, show that more than one equilibrium solutions bifurcate from the equilibrium solution $x = 0$ when $\varepsilon = 0$.

6. $\dot{x}_1 = \varepsilon x_1 - \varepsilon x_2 - x_1^2 + x_2^2$
$\dot{x}_2 = \varepsilon x_2 + x_1 x_2$

7. $\dot{x}_1 = \varepsilon x_1 - x_1^2 - x_1 x_2$
$\dot{x}_2 = -2\varepsilon x_1 + 2\varepsilon x_2 + x_1 x_2 - x_2^2$

8. $\dot{x}_1 = \varepsilon x_2 + x_1 x_2$
$\dot{x}_2 = -\varepsilon x_1 + \varepsilon x_2 + x_1^2 + x_2^2$

9. Consider the system of equations
$\dot{x}_1 = 3\varepsilon x_1 - 5\varepsilon x_2 - x_1^2 + x_2^2$
$\dot{x}_2 = 2\varepsilon x_1 - \varepsilon x_2.$ $\qquad (*)$

(a) Show that each point on the lines $x_2 = x_1$ and $x_2 = -x_1$ are equilibrium points of $(*)$ for $\varepsilon = 0$.

(b) Show that

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \tfrac{7}{3}\varepsilon \begin{pmatrix} 1 \\ 2 \end{pmatrix}.$$

are the only equilibrium points of $(*)$ for $\varepsilon \neq 0$.

10. Show that

$$x^1 = \begin{pmatrix} 1 + \sqrt{1+\varepsilon} \\ 1 \end{pmatrix} \quad \text{and} \quad x^2 = \begin{pmatrix} 1 - \sqrt{1+\varepsilon} \\ 1 \end{pmatrix}$$

are eigenvectors of the matrix $\begin{pmatrix} 1 & \varepsilon \\ 1 & -1 \end{pmatrix}$ with eigenvalues $\sqrt{1+\varepsilon}$ and $-\sqrt{1+\varepsilon}$ respectively.

4.10 Predator–prey problems; or why the percentage of sharks caught in the Mediterranean Sea rose dramatically during World War I

In the mid 1920's the Italian biologist Umberto D'Ancona was studying the population variations of various species of fish that interact with each other. In the course of his research, he came across some data on per-

centages-of-total-catch of several species of fish that were brought into different Mediterranean ports in the years that spanned World War I. In particular, the data gave the percentage-of-total-catch of selachians, (sharks, skates, rays, etc.) which are not very desirable as food fish. The data for the port of Fiume, Italy, during the years 1914–1923 is given below.

1914	1915	1916	1917	1918
11.9%	21.4%	22.1%	21.2%	36.4%

1919	1920	1921	1922	1923
27.3%	16.0%	15.9%	14.8%	10.7%

D'Ancona was puzzled by the very large increase in the percentage of selachians during the period of the war. Obviously, he reasoned, the increase in the percentage of selachians was due to the greatly reduced level of fishing during this period. But how does the intensity of fishing affect the fish populations? The answer to this question was of great concern to D'Ancona in his research on the struggle for existence between competing species. It was also of concern to the fishing industry, since it would have obvious implications for the way fishing should be done.

Now, what distinguishes the selachians from the food fish is that the selachians are predators, while the food fish are their prey; the selachians depend on the food fish for their survival. At first, D'Ancona thought that this accounted for the large increase of selachians during the war. Since the level of fishing was greatly reduced during this period, there were more prey available to the selachians, who therefore thrived and multiplied rapidly. However, this explanation does not hold any water since there were also more food fish during this period. D'Ancona's theory only shows that there are more selachians when the level of fishing is reduced; it does not explain why a reduced level of fishing is *more* beneficial to the predators than to their prey.

After exhausting all possible biological explanations of this phenomenon, D'Ancona turned to his colleague, the famous Italian mathematician Vito Volterra. Hopefully, Volterra would formulate a mathematical model of the growth of the selachians and their prey, the food fish, and this model would provide the answer to D'Ancona's question. Volterra began his analysis of this problem by separating all the fish into the prey population $x(t)$ and the predator population $y(t)$. Then, he reasoned that the food fish do not compete very intensively among themselves for their food supply since this is very abundant, and the fish population is not very dense. Hence, in the absence of the selachians, the food fish would grow according to the Malthusian law of population growth $\dot{x} = ax$, for some positive constant a. Next, reasoned Volterra, the number of contacts per unit time between predators and prey is bxy, for some positive constant b. Hence, $\dot{x} = ax - bxy$. Similarly, Volterra concluded that the predators have a natural rate of decrease $-cy$ proportional to their present number, and

that they also increase at a rate dxy proportional to their present number y and their food supply x. Thus,

$$\frac{dx}{dt} = ax - bxy, \qquad \frac{dy}{dt} = -cy + dxy. \tag{1}$$

The system of equations (1) governs the interaction of the selachians and food fish in the absence of fishing. We will carefully analyze this system and derive several interesting properties of its solutions. Then, we will include the effect of fishing in our model, and show why a reduced level of fishing is more beneficial to the selachians than to the food fish. In fact, we will derive the surprising result that a reduced level of fishing is actually harmful to the food fish.

Observe first that (1) has two equilibrium solutions $x(t) = 0, y(t) = 0$ and $x(t) = c/d, y(t) = a/b$. The first equilibrium solution, of course, is of no interest to us. This system also has the family of solutions $x(t) = x_0 e^{at}, y(t) = 0$ and $x(t) = 0, y(t) = y_0 e^{-ct}$. Thus, both the x and y axes are orbits of (1). This implies that every solution $x(t), y(t)$ of (1) which starts in the first quadrant $x > 0, y > 0$ at time $t = t_0$ will remain there for all future time $t \geqslant t_0$.

The orbits of (1), for $x, y \neq 0$ are the solution curves of the first-order equation

$$\frac{dy}{dx} = \frac{-cy + dxy}{ax - bxy} = \frac{y(-c + dx)}{x(a - by)}. \tag{2}$$

This equation is separable, since we can write it in the form

$$\frac{a - by}{y} \frac{dy}{dx} = \frac{-c + dx}{x}.$$

Consequently, $a \ln y - by + c \ln x - dx = k_1$, for some constant k_1. Taking exponentials of both sides of this equation gives

$$\frac{y^a}{e^{by}} \frac{x^c}{e^{dx}} = K \tag{3}$$

for some constant K. Thus, the orbits of (1) are the family of curves defined by (3), and these curves are *closed* as we now show.

Lemma 1. *Equation* (3) *defines a family of closed curves for* $x, y > 0$.

Proof. Our first step is to determine the behavior of the functions $f(y) = y^a / e^{by}$ and $g(x) = x^c / e^{dx}$ for x and y positive. To this end, observe that $f(0) = 0, f(\infty) = 0$, and $f(y)$ is positive for $y > 0$. Computing

$$f'(y) = \frac{ay^{a-1} - by^a}{e^{by}} = \frac{y^{a-1}(a - by)}{e^{by}},$$

we see that $f(y)$ has a single critical point at $y = a/b$. Consequently, $f(y)$ achieves its maximum value $M_y = (a/b)^a / e^a$ at $y = a/b$, and the graph of
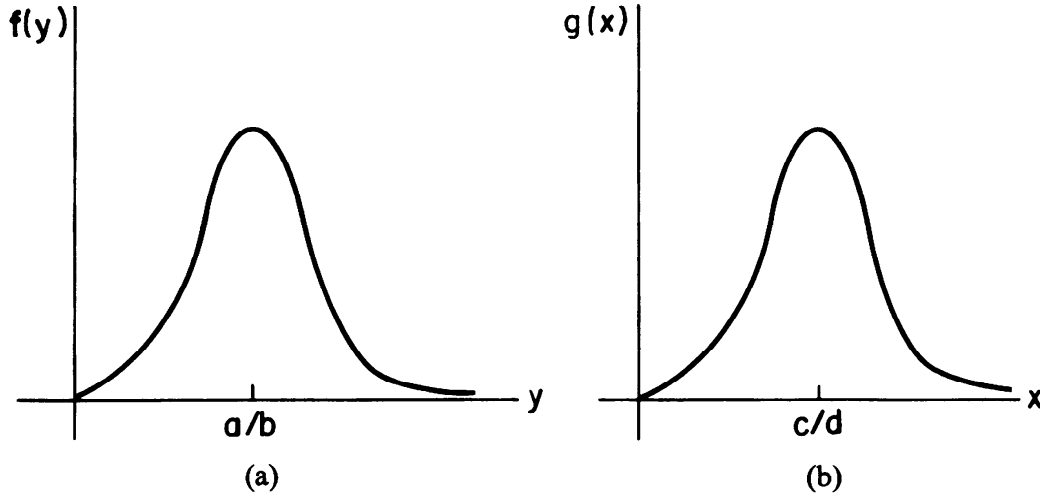
443

Figure 1. (a) Graph of $f(y)=y^a e^{-by}$; (b) Graph of $g(x)=x^c e^{-dx}$

$f(y)$ has the form described in Figure 1a. Similarly, $g(x)$ achieves its maximum value $M_x=(c/d)^c/e^c$ at $x=c/d$, and the graph of $g(x)$ has the form described in Figure 1b.

From the preceding analysis, we conclude that Equation (3) has no solution $x,y>0$ for $K>M_x M_y$, and the single solution $x=c/d, y=a/b$ for $K = M_x M_y$. Thus, we need only consider the case $K=\lambda M_y$, where λ is a positive number less than M_x. Observe first that the equation $x^c/e^{dx}=\lambda$ has one solution $x=x_m<c/d$, and one solution $x=x_M>c/d$. Hence, the equation

$$f(y)=y^a e^{-by}=\left(\frac{\lambda}{x^c e^{-dx}}\right)M_y$$

has no solution y when x is less than x_m or greater than x_M. It has the single solution $y=a/b$ when $x=x_m$ or x_M, and it has two solutions $y_1(x)$ and $y_2(x)$ for each x between x_m and x_M. The smaller solution $y_1(x)$ is always less than a/b, while the larger solution $y_2(x)$ is always greater than a/b. As x approaches either x_m or x_M, both $y_1(x)$ and $y_2(x)$ approach a/b. Consequently, the curves defined by (3) are closed for x and y positive, and have the form described in Figure 2. Moreover, none of these closed curves (with the exception of $x=c/d, y=a/b$) contain any equilibrium points of (1). Therefore, all solutions $x(t)$, $y(t)$ of (1), with $x(0)$ and $y(0)$ positive, are *periodic* functions of time. That is to say, each solution $x(t)$, $y(t)$ of (1), with $x(0)$ and $y(0)$ positive, has the property that $x(t+T)=x(t)$ and $y(t+T)=y(t)$ for some positive T. □

Now, the data of D'Ancona is really an *average* over each one year period of the proportion of predators. Thus, in order to compare this data with the predictions of (1), we must compute the "average values" of $x(t)$ and $y(t)$, for any solution $x(t)$, $y(t)$ of (1). Remarkably, we can find these average values even though we cannot compute $x(t)$ and $y(t)$ exactly. This is the content of Lemma 2.
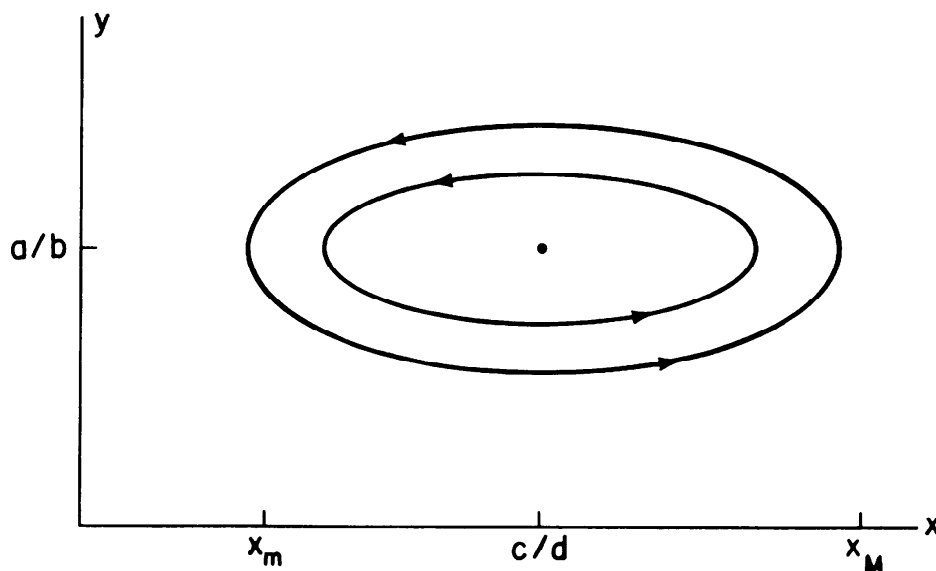
Figure 2. Orbits of (1) for x,y positive

Lemma 2. *Let* $x(t)$, $y(t)$ *be a periodic solution of* (1), *with period* $T > 0$. *Define the average values of* x *and* y *as*

$$\bar{x} = \frac{1}{T}\int_0^T x(t)\,dt, \qquad \bar{y} = \frac{1}{T}\int_0^T y(t)\,dt.$$

Then, $\bar{x} = c/d$ *and* $\bar{y} = a/b$. *In other words, the average values of* $x(t)$ *and* $y(t)$ *are the equilibrium values.*

PROOF. Dividing both sides of the first equation of (1) by x gives $\dot{x}/x = a - by$, so that

$$\frac{1}{T}\int_0^T \frac{\dot{x}(t)}{x(t)}\,dt = \frac{1}{T}\int_0^T \left[a - by(t)\right] dt.$$

Now, $\int_0^T \dot{x}(t)/x(t)\,dt = \ln x(T) - \ln x(0)$, and this equals zero since $x(T) = x(0)$. Consequently,

$$\frac{1}{T}\int_0^T by(t)\,dt = \frac{1}{T}\int_0^T a\,dt = a,$$

so that $\bar{y} = a/b$. Similarly, by dividing both sides of the second equation of (1) by $Ty(t)$ and integrating from 0 to T, we obtain that $\bar{x} = c/d$. $\qquad\square$

We are now ready to include the effects of fishing in our model. Observe that fishing decreases the population of food fish at a rate $\varepsilon x(t)$, and decreases the population of selachians at a rate $\varepsilon y(t)$. The constant ε reflects the intensity of fishing; i.e., the number of boats at sea and the number of nets in the water. Thus, the true state of affairs is described by the

modified system of differential equations

$$\frac{dx}{dt} = ax - bxy - \varepsilon x = (a - \varepsilon)x - bxy$$

$$\frac{dy}{dt} = -cy + dxy - \varepsilon y = -(c + \varepsilon)y + dxy. \tag{4}$$

This system is exactly the same as (1) (for $a - \varepsilon > 0$), with a replaced by $a - \varepsilon$, and c replaced by $c + \varepsilon$. Hence, the average values of $x(t)$ and $y(t)$ are now

$$\bar{x} = \frac{c + \varepsilon}{d}, \qquad \bar{y} = \frac{a - \varepsilon}{b}. \tag{5}$$

Consequently, a moderate amount of fishing ($\varepsilon < a$) actually increases the number of food fish, on the average, and decreases the number of selachians. Conversely, a reduced level of fishing increases the number of selachians, on the average, and *decreases* the number of food fish. This remarkable result, which is known as Volterra's principle, explains the data of D'Ancona, and completely solves our problem.

Volterra's principle has spectacular applications to insecticide treatments, which destroy both insect predators and their insect prey. It implies that the application of insecticides will actually increase the population of those insects which are kept in control by other predatory insects. A remarkable confirmation comes from the cottony cushion scale insect (Icerya purchasi), which, when accidentally introduced from Australia in 1868, threatened to destroy the American citrus industry. Thereupon, its natural Australian predator, a ladybird beetle (Novius Cardinalis) was introduced, and the beetles reduced the scale insects to a low level. When DDT was discovered to kill scale insects, it was applied by the orchardists in the hope of further reducing the scale insects. However, in agreement with Volterra's principle, the effect was an increase of the scale insect!

Oddly enough, many ecologists and biologists refused to accept Volterra's model as accurate. They pointed to the fact that the oscillatory behavior predicted by Volterra's model is not observed in most predator–prey systems. Rather, most predator–prey systems tend to equilibrium states as time evolves. Our answer to these critics is that the system of differential equations (1) is not intended as a model of the general predator–prey interaction. This is because the food fish and selachians do not compete intensively among themselves for their available resources. A more general model of predator–prey interactions is the system of differential equations

$$\dot{x} = ax - bxy - ex^2, \qquad \dot{y} = -cy + dxy - fy^2. \tag{6}$$

Here, the term ex^2 reflects the internal competition of the prey x for their limited external resources, and the term fy^2 reflects the competition among the predators for the limited number of prey. The solutions of (6) are not, in general, periodic. Indeed, we have already shown in Example 1 of Sec-

tion 4.8 that all solutions $x(t)$, $y(t)$ of (6), with $x(0)$ and $y(0)$ positive, ultimately approach the equilibrium solution $x = a/e$, $y = 0$ if c/d is greater than a/e. In this situation, the predators die out, since their available food supply is inadequate for their needs.

Surprisingly, some ecologists and biologists even refuse to accept the more general model (6) as accurate. As a counterexample, they cite the experiments of the mathematical biologist G. F. Gause. In these experiments, the population was composed of two species of protozoa, one of which, Didinium nasatum, feeds on the other, Paramecium caudatum. In all of Gause's experiments, the Didinium quickly destroyed the Paramecium and then died of starvation. This situation cannot be modeled by the system of equations (6), since no solution of (6) with $x(0)y(0) \neq 0$ can reach $x = 0$ or $y = 0$ in finite time.

Our answer to these critics is that the Didinium are a special, and atypical type of predator. On the one hand, they are ferocious attackers and require a tremendous amount of food; a Didinium demands a fresh Paramecium every three hours. On the other hand, the Didinium don't perish from an insufficient supply of Paramecium. They continue to multiply, but give birth to smaller offspring. Thus, the system of equations (6) does not accurately model the interaction of Paramecium and Didinium. A better model, in this case, is the system of differential equations

$$\frac{dx}{dt} = ax - b\sqrt{x}\ y, \qquad \frac{dy}{dt} = \begin{cases} d\sqrt{x}\ y, & x \neq 0 \\ -cy, & x = 0 \end{cases}. \tag{7}$$

It can be shown (see Exercise 6) that every solution $x(t)$, $y(t)$ of (7) with $x(0)$ and $y(0)$ positive reaches $x = 0$ in finite time. This does not contradict the existence–uniqueness theorem, since the function

$$g(x,y) = \begin{cases} d\sqrt{x}\ y, & x \neq 0 \\ -cy, & x = 0 \end{cases}$$

does not have a partial derivative with respect to x or y, at $x = 0$.

Finally, we mention that there are several predator–prey interactions in nature which cannot be modeled by any system of ordinary differential equations. These situations occur when the prey are provided with a refuge that is inaccessible to the predators. In these situations, it is impossible to make any definitive statements about the future number of predators and prey, since we cannot predict how many prey will be stupid enough to leave their refuge. In other words, this process is now *random*, rather than *deterministic*, and therefore cannot be modeled by a system of ordinary differential equations. This was verified directly in a famous experiment of Gause. He placed five Paramecium and three Didinium in each of thirty identical test tubes, and provided the Paramecium with a refuge from the Didinium. Two days later, he found the predators dead in four tubes, and a mixed population containing from two to thirty-eight Paramecium in the remaining twenty-six tubes.

Reference

Volterra, V: "Leçons sur la théorie mathématique de la lutte pour la vie." Paris, 1931.

EXERCISES

1. Find all biologically realistic equilibrium points of (6) and determine their stability.

2. We showed in Section 4.8 that $y(t)$ ultimately approaches zero for all solutions $x(t), y(t)$ of (6), if $c/d > a/e$. Show that there exist solutions $x(t), y(t)$ of (6) for which $y(t)$ increases at first to a maximum value, and then decreases to zero. (To an observer who sees only the predators without noticing the prey, such a case of a population passing through a maximum to total extinction would be very difficult to explain.)

3. In many instances, it is the adult members of the prey who are chiefly attacked by the predators, while the young members are better protected, either by their smaller size, or by their living in a different station. Let x_1 be the number of adult prey, x_2 the number of young prey, and y the number of predators. Then,

$$\dot{x}_1 = -a_1 x_1 + a_2 x_2 - b x_1 y$$
$$\dot{x}_2 = n x_1 - (a_1 + a_2) x_2$$
$$\dot{y} = -cy + d x_1 y$$

where $a_2 x_2$ represents the number of young (per unit time) growing into adults, and n represents the birth rate proportional to the number of adults. Find all equilibrium solutions of this system.

4. There are several situations in nature where species 1 preys on species 2 which in turn preys on species 3. One case of this kind of population is the Island of Komodo in Malaya which is inhabited by giant carnivorous reptiles, and by mammals—their food—which feed on the rich vegetation of the island. We assume that the reptiles have no direct influence on the vegetation, and that only the plants compete among themselves for their available resources. A system of differential equations governing this interaction is

$$\dot{x}_1 = -a_1 x_1 - b_{12} x_1 x_2 + c_{13} x_1 x_3$$
$$\dot{x}_2 = -a_2 x_2 + b_{21} x_1 x_2$$
$$\dot{x}_3 = a_3 x_3 - a_4 x_3^2 - c_{31} x_1 x_3$$

Find all equilibrium solutions of this system.

5. Consider a predator–prey system where the predator has alternate means of support. This system can be modelled by the differential equations

$$\dot{x}_1 = \alpha_1 x_1 (\beta_1 - x_1) + \gamma_1 x_1 x_2$$
$$\dot{x}_2 = \alpha_2 x_2 (\beta_2 - x_2) - \gamma_2 x_1 x_2$$

where $x_1(t)$ and $x_2(t)$ are the predators and prey populations, respectively, at time t.

(a) Show that the change of coordinates $\beta_i y_i(t) = x_i(t/\alpha_i \beta_i)$ reduces this system of equations to

$$\dot{y}_1 = y_1(1 - y_1) + a_1 y_1 y_2, \qquad \dot{y}_2 = y_2(1 - y_2) - a_2 y_1 y_2$$

where $a_1 = \gamma_1 \beta_2 / \alpha_1 \beta_1$ and $a_2 = \gamma_2 \beta_1 / \alpha_2 \beta_2$.

(b) What are the stable equilibrium populations when (i) $0 < a_2 < 1$, (ii) $a_2 > 1$?

(c) It is observed that $a_1 = 3a_2$ (a_2 is a measure of the aggressiveness of the predator). What is the value of a_2 if the predator's instinct is to maximize its stable equilibrium population?

6. (a) Let $x(t)$ be a solution of $\dot{x} = ax - M\sqrt{x}$, with $M > a\sqrt{x(t_0)}$. Show that

$$a\sqrt{x} = M - \left(M - a\sqrt{x(t_0)} \right) e^{a(t - t_0)/2}.$$

(b) Conclude from (a) that $x(t)$ approaches zero in finite time.

(c) Let $x(t), y(t)$ be a solution of (7), with $by(t_0) > a\sqrt{x(t_0)}$. Show that $x(t)$ reaches zero in finite time. *Hint*: Observe that $y(t)$ is increasing for $t > t_0$.

(d) It can be shown that $by(t)$ will eventually exceed $a\sqrt{x(t)}$ for every solution $x(t), y(t)$ of (7) with $x(t_0)$ and $y(t_0)$ positive. Conclude, therefore, that all solutions $x(t), y(t)$ of (7) achieve $x = 0$ in finite time.

4.11 The principle of competitive exclusion in population biology

It is often observed, in nature, that the struggle for existence between two similar species competing for the same limited food supply and living space nearly always ends in the complete extinction of one of the species. This phenomenon is known as the "principle of competitive exclusion." It was first enunciated, in a slightly different form, by Darwin in 1859. In his paper 'The origin of species by natural selection' he writes: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitutions and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera."

There is a very interesting biological explanation of the principle of competitive exclusion. The cornerstone of this theory is the idea of a "niche." A niche indicates what place a given species occupies in a community; i.e., what are its habits, food and mode of life. It has been observed that as a result of competition two similar species rarely occupy the same niche. Rather, each species takes possession of those kinds of food and modes of life in which it has an advantage over its competitor. If the two species tend to occupy the same niche then the struggle for existence between them will be very intense and result in the extinction of the weaker species.

An excellent illustration of this theory is the colony of terns inhabiting the island of Jorilgatch in the Black Sea. This colony consists of four different species of terns: sandwich-tern, common-tern, blackbeak-tern, and lit-