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FEEDBACK IN PALEOECOLOGICAL SYSTEMS

John W. Harbaugh and Graeme Bonham-Carter

Department of Geology, Stanford University, Palo Alto, Calif., USA

INTRODUCTION

The theory of systems has an important bearing on the study of ecology. The relationships between organisms and their environment constitute a natural system, called by Tansley (1935) an ecosystem. Fosberg (1963) describes an ecosystem as a "functioning interacting system composed of one or more living organisms and their effective environment . . . The description of an ecosystem may include its spatial relations; inventories of its physical features, its habitats and ecological niches, its organisms and its basic reserves of matter and energy; its patterns of circulation of matter and energy; the nature of its income (input) of matter and energy; and the behavior or trend of its energy level."

FEEDBACK

Probably the most important single concept of systems theory is the idea of feedback. As the word implies, this pertains to the "feeding back" of signals of various forms, thereby influencing the subsequent course of a process by means of a closed-loop (Fig. 1).

Feedback is ubiquitous not only in ecological systems, but in economic, chemical, mechanical, electrical systems amongst many others. Table I illustrates a few common examples.

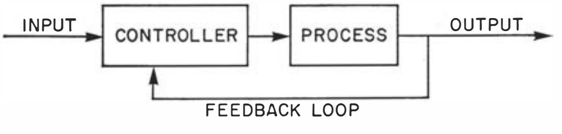

Fig. 1. Diagram of a feedback loop. The *process* by which *input* is transformed to *output* is governed by a *controller*. The controller is influenced by information signals which are fed back from the output by a closed loop.

There are two principal forms of feedback: (1) negative feedback which is essential in all dynamic systems because it exerts basic control, and (2) positive feedback, which may or may not be present, and which is necessarily temporary.

Negative feedback

As its name implies negative feedback causes a reversal of a previous condition. A familiar example is the interaction between a household furnace and thermostat. As the house grows cold, the thermostat feeds a signal to the furnace, which causes the furnace to supply heat. When the house is sufficiently warm, the thermostat shuts off the furnace. Subsequent loss of heat from the house then prompts another cycle round this 'closed' loop. All simple negative feedback loops (the furnace/thermostat system is a simple loop) exhibit oscillation. In more advanced systems, oscillation may be damped, but not eliminated. An example of output from a computer model of a simple furnace/thermostat system is shown in Fig. 2. The tempera-

Table I. *Some examples of feedback in systems*

System	Negative Feedback	Positive Feedback
Familiar systems	House heating control furnace/thermostat	Economic inflation wages/prices spiral
Ecological systems	Biological control prey/predator	Initiation of coral reef growth (epidemic effect) corals/shallow water
Chemical systems	Chemical control buffers	Combustion temperature/ignition
Mechanical systems	Steam engine control flywheel "governor"	Hydraulic brakes decrease in speed/increase in brake pressure

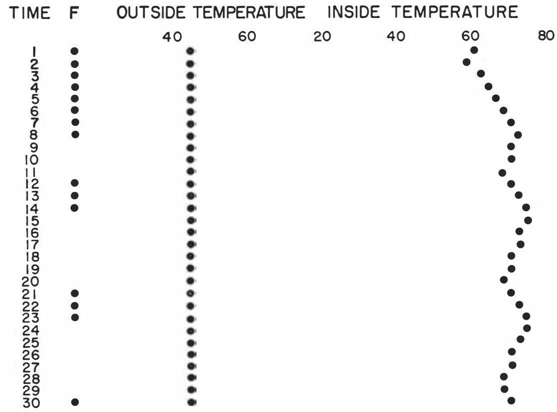

Fig. 2. Output from a simple computer model of furnace/thermostat interaction. During each time step the furnace (F) is either on (*) or off ( ). In this example the outside temperature was held constant at 40°, the thermostat was set at 70° and the initial inside temperature was 60°. Due to a built in response time lag the inside temperature exhibits oscillation.

ture oscillates in regular fashion because of the periodic on–off relationship of the thermostat's signal.

An example of negative feedback in a simple ecological system, adapted from Garfinkel *et al.* (1964), is illustrated in Figs. 3 and 4. This model describes mathematically a prey/predator interrelationship in which rabbits eat grass, and in turn, foxes eat rabbits. In spite of the simplicity of this model, the response is surprisingly complex. The initial situation is that of a rabbit/grass relationship involving rabbits which may be fed,

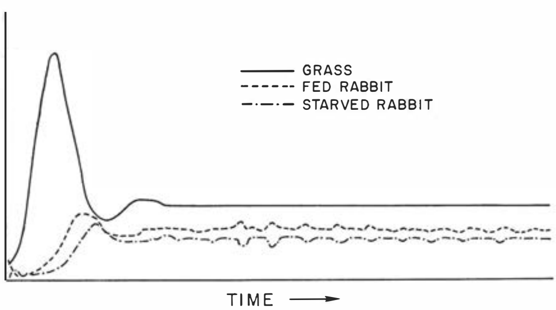

Fig. 3. Behavior of a simple hypothetical ecological system composed of grass and rabbits. The rabbits eat grass and are either 'fed' or 'starved'. After an initial increase in grass, closely followed by an increase in fed rabbits, the grass decreased, the starved rabbits increased, then all three components settled near equilibrium. From Garfinkel *et al.* (1964).

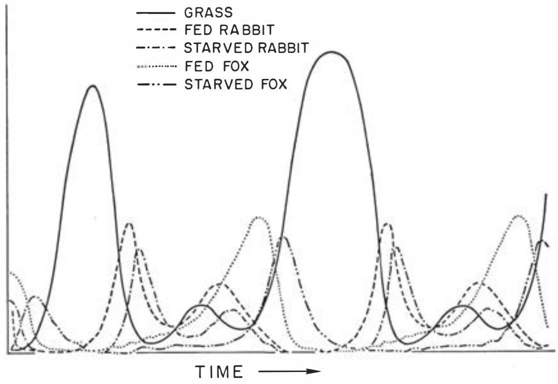

Fig. 4. Behavior of a more complex prey/predator system. Not only do rabbits eat grass, but foxes eat rabbits. This system exhibits complex oscillations due to the double feedback loop. From Garfinkel *et al.* (1964).

or may be starved (due to inaccessibility of grass). By adjusting the parameters in the model, a more or less stable system is rapidly reached (Fig. 3). When, however, the system is complicated by the introduction of a predator (foxes), the system exhibits complex oscillations (Fig. 4).

The prey/predator interaction of Figs. 3 and 4 reflect both negative and positive feedback relationships. Positive feedback is manifest when a temporarily rising rabbit population begets a temporarily rising fox population. In time, however, the rabbit population declines, exerting a negative feedback effect on the fox population.

Positive Feedback

Probably the most familiar example of positive feedback is economic inflation. Rising wages increase production costs which cause prices to rise, which in turn raises the cost of living, which promotes a rise in wages, and so on. Quite clearly positive feedback is not a controlling influence, and does not keep the system in equilibrium.

Positive feedback is less obvious in nature than negative feedback, but is nevertheless important. The epidemic effect of coral reef growth in a warm water environment is an important example (Harbaugh, 1966). Two types of positive feedback are present here. First the colonization of a sea bottom by coral polyps starts as a series of isolated patches. Having once started, however, the chances of polyp production and survival increases as in an epidemic, both because of the increased numbers of individuals and the more favorable substrate for their anchorage. Secondly, assuming that colonization starts at the maximum tolerable depth, increasingly favorable conditions are encountered by decreasing water depth. Thus as the coral reef grows upwards, the coral environment becomes more favorable, which causes more vigorous upward growth, and so on. In this case a limit is reached once low tide level is attained, and a negative feedback controls further upward growth.

SIMULATION OF DYNAMIC SYSTEMS

Conceptual models, particularly in the form of diagrams are useful ways of displaying systems components and their inter-relationships. Feedback loops and interconnecting lines, the recognition of points of input and output, of exogenous and endogenous variables, may all be displayed in diagram form. A conceptual model is limited in that it may fail to indicate quantitative relationships and because it lacks the dynamic character so important in natural systems.

With the advent of high speed computers, it is now possible to set up computer models, written in a programming language such as FORTRAN or ALGOL, which *simulate* the behavior of systems mathematically. The flow chart of the computer program will be very similar to the block diagrams of conceptual models. Programming languages are especially well-suited for representative feedback loops, for example, the DO-loop of FORTRAN. In addition, complex equations or simple but time-consuming accounting operations may be accomplished in fractions of a second.

Equipped with a computer model of an ecological system, the researcher may wish to pose questions such as "what effect will the introduction of a predator have on the rabbit/grass system", as discussed above. The answer to this question was provided by using a mathematical model which simulated the behavior of grass/rabbit/fox relationships. The enormous economic advantages to be gained by making preliminary experimental studies of ecological systems has stimulated considerable activity in this field; see Watt (1966).

For palaeoecology, simulation models are useful for exploring sets of alternative hypotheses and assumptions. Fox (1967) has used a simulation approach to study time trend variations in brachiopod genera in an Ordovician limestone sequence. Using a much more complex model, Harbaugh (1966) has simulated the behavior of seafloor "communities" in an algal bank environment in an area in Kansas during Pennsylvanian time.

Sommaire. La théorie des systhèmes de contrôle formel peut être appliquée à des populations écologiques et paléoécologiques. Un « feedback » négatif entre dans tous les systhèmes de contrôle. Tout comme indique son nom, il amène un changement de la condition primaire en reliant, par un retour de « feedback », le processus contrôlé au mécanisme qui sert pour le contrôle. Souvent, ces retours de « feedback » simples et négatifs tendent à osciller à cause de l'action réciproque du processus et du mécanisme contrôleur.

Des populations d'organismes, surtout si ceux-ci vivent dans des relations de proies et de prédateurs, peuvent être considérées comme composantes des retours de « feedback » négatifs. Les variations de dimension de la population des proies agissent sur les dimensions de la population prédatrice et réciproquement. Les fluctuations qui en résultent pour les dimensions des deux populations peuvent être complexes, parce que celles-ci sont reliées l'une à l'autre en un retour de « feedback » négatif. Les ordinateurs qui peuvent automatiquement rendre compte des mebres individuels de populations agissant l'une sur l'autre rendent bon service dans la recherche de différentes explications sur les variations de dimensions des populations.

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