

Therefore the probability density function for the Debbie results, if hypothesis H_i is true, now becomes

$$P'(69\%, 85\%|H_i) = \begin{cases} 1.4996 & i = 1 \\ 0.5716 & i = 2 \\ 0.2827 & i = 3 \end{cases} \quad (4)$$

Now, considering the deductions made in (2)—on the basis of physical reasoning and the results of numerical model experiments which definitely indicate an effect of intensification by seeding—I assign the pre-Debbie probabilities

$$\begin{aligned} P'(H_1) &= .0227 \\ P'(H_2) &= .7500 \\ P'(H_3) &= .2273 \end{aligned} \quad (5)$$

whereas in Howard *et al.* the corresponding set is

$$\begin{aligned} P(H_1) &= .15 \\ P(H_2) &= .75 \\ P(H_3) &= .10 \end{aligned}$$

Hence, the pre-Debbie odds that seeding has no effect are the same in set 5 as in Howard *et al.* However, $P'(H_3)$ is taken to be one order of magnitude larger than $P'(H_1)$ to reflect that, if seeding affects the intensity at all, an increase of the maximum wind is expected.

When sets 4 and 5 are introduced in Bayes' equation the posterior probabilities become

$$\begin{aligned} P'(H_1) &= .0647 \\ P'(H_2) &= .8131 \\ P'(H_3) &= .1222 \end{aligned} \quad (6)$$

whereas in Howard *et al.*

$$\begin{aligned} P(H_1) &= .49 \\ P(H_2) &= .49 \\ P(H_3) &= .02 \end{aligned}$$

Set 6 implies that, since the Debbie results, the odds are about 4 to 1 that seeding has no effect, and if seeding does have an effect the odds are 2 to 1 for wind intensification rather than wind reduction.

Finally, I can compute the probability distribution on wind speed [from Eqs. 1, 2, 3, and 6 above and equation 4 in (1)]. The difference in probability between the seeding and not-seeding alternatives is so small that it is hard to show it in a plot of the complementary cumulative distribution functions of those two alternatives. Instead, I plot this function for the not-seeding alternative and the difference (the function for seeding minus the function for not-seeding) in Fig. 1. I find that the probability for intensification (wind speed more than 100 percent of the initial wind speed) if a hurricane is

seeded is .511; if the hurricane is not seeded the probability is .500 [in (1) these values are .36 and .50, respectively]. The probability of intensification by 10 percent or more is .278 if a hurricane is seeded and .261 if it is not seeded [.18 and .26, respectively, in (1)].

Furthermore, for any particular wind speed larger than 88 percent of its initial value, the probability that this speed will be exceeded is greater if the hurricane is seeded than if it is not seeded. For wind speeds less than 88 percent of their initial values the situation is reversed; however, the difference in this interval is much smaller in magnitude than it is in the former interval.

Since the analysis given above may be considered to be as soundly based as that in (1), it shows that the available data are too sparse to yield a statistical basis for conclusive statements. I suggest that the method of statistical analysis (possibly somewhat modified) should be used to investigate the requirements on reliability and volume of results from model studies and field experiments in order to permit confident conclusions and recommendations.

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References and Notes

1. R. A. Howard, J. E. Matheson, D. W. North, *Science* **176**, 1191 (1972).
2. H. Sundqvist, *Tellus* **24** (No. 1), 6 (1972).
3. The same notation is used here as in (1). For convenience, some of the data given in (1) are repeated; the probabilities from that article are designated by P and those of the treatment given here by P' .
4. As in Howard *et al.* [reference 13 in (1)] a probability distribution on a quantity x is denoted $P(x)$, and a probability distribution of the normal or Gaussian family specified by its mean m and standard deviation σ is denoted $f_N(m, \sigma)$.

31 October 1972; revised 1 June 1973

In the concluding section of our article we stated: "The results of a decision analysis depend on the infor-

mation available at the time it is performed. Decision analysis should not be used to arrive at a static recommendation to be verified by further research, rather it should be used as a dynamic tool for making necessary decisions at any time." We are pleased that Sundqvist finds our analysis a useful format in which to present his views regarding the results of hurricane modification. He has succinctly summarized his opinion in the form of a prior probability distribution and then used the Debbie experimental results to develop consequent probability distributions for the wind speed, both with and without seeding. His pre-Debbie probability assignment was that there was a 75 percent chance of no seeding effect, and that if there were an effect, the odds were 10 to 1 that it would be deleterious. The Debbie experiment is not sufficient to overcome this pessimistic prior probability distribution: a decision-maker who subscribed to Sundqvist's view would not wish to attempt operational hurricane seeding at this time.

Our analysis was based on the best information we could obtain from U.S. hurricane modification experts. As decision analysts we cannot comment on Sundqvist's differing opinion, except to say that our information sources were aware of his work and did not subscribe to his views. Further dialogue between Sundqvist and the community of U.S. hurricane modification experts would be appropriate to determine whether the latter see any new reason to modify their judgments.

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24 April 1973; revised 18 June 1973

Stable Limit Cycles in Prey-Predator Populations

In a recent report (1) May discussed several mathematical models of prey-predator population interactions, all variants of the Kolmogorov model (2). May attributed to Kolmogorov the statement that this model possesses either a stable equilibrium point or a stable limit cycle (3). Kolmogorov (2) has remarked, however, that under his own hypotheses there may be sev-

eral possible configurations, one of which is an unstable equilibrium point that is surrounded by an uncountable number of neutrally stable periodic solutions (hence neither a stable equilibrium point nor a stable limit cycle).

In the same report (1), May claimed that his interpretation of Kolmogorov's results holds under even more general

hypotheses. We show here that this assertion is incorrect.

Let x denote the prey population size, y the predator population size, and $g(x,y)$, $h(x,y)$ their respective fractional (or per individual) growth rates. The dynamic equations describing the interactions are

$$\frac{dx}{dt} = xg(x,y) \quad (1a)$$

$$\frac{dy}{dt} = yh(x,y) \quad (1b)$$

These equations, where g and h satisfy Kolmogorov's hypotheses [equations 3 through 9 in (1)], constitute the Kolmogorov model. Here we assume that g and h are continuous in the closed first quadrant ($x \geq 0$, $y \geq 0$), have continuous partial derivatives in the interior of the first quadrant ($x > 0$, $y > 0$), and satisfy the following hypotheses:

$$\frac{\partial g}{\partial y} < 0, \quad x \frac{\partial g}{\partial x} + y \frac{\partial g}{\partial y} < 0$$

for $x > 0$, $y > 0$

$$\frac{\partial h}{\partial y} \leq 0, \quad x \frac{\partial h}{\partial x} + y \frac{\partial h}{\partial y} > 0$$

for $x > 0$, $y > 0$

In addition there exist $A > 0$, $B > 0$, $C > 0$ such that

$$\begin{aligned} g(0,y) &> 0 \text{ for } 0 \leq y < A \\ &< 0 \text{ for } y > A \\ g(x,0) &> 0 \text{ for } 0 \leq x < B \\ &< 0 \text{ for } x > B \\ h(x,0) &< 0 \text{ for } 0 \leq x < C \\ &> 0 \text{ for } x > C \\ B &> C \end{aligned}$$

We have assumed the above hypotheses rather than Kolmogorov's conditions or May's relaxed conditions [given in reference 17 of (1)]. Kolmogorov's conditions, which are to hold in the closed quadrant ($x \geq 0$, $y \geq 0$), lead to the contradiction $(\partial h / \partial y) < 0$ and $(\partial h / \partial y) > 0$ on the positive y -axis. Furthermore, if Kolmogorov's conditions are satisfied for $x > 0$, $y > 0$, then our hypotheses will hold, and, in turn, if our hypotheses are met, then May's relaxed conditions will be satisfied for $x > 0$, $y > 0$.

We now give an example which satisfies our hypotheses and has neither a stable equilibrium point nor a stable limit cycle, thereby disproving May's assertion. In Eqs. 1a and 1b let

$$h(x,y) = \lambda_2 x - a_2 \quad (2a)$$

$$g(x,y) = a_1 - \lambda_1 y + c(x - x_e)\varphi(x - x_e) \quad (2b)$$

$$\begin{aligned} \varphi(y - y_e) &\text{ if } 0 \leq x \leq \tilde{x} \\ g(x,y) &= a_1 - \lambda_1 y - (x - \tilde{x})^2 \text{ if } x > \tilde{x} \end{aligned} \quad (2c)$$

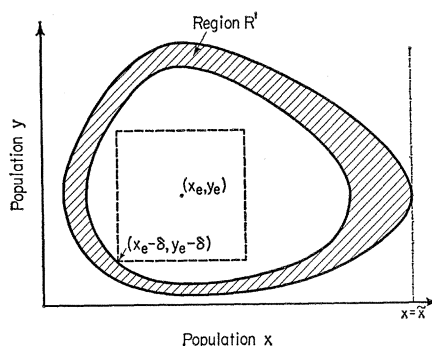


Fig. 1. All the periodic solutions of Eqs. 1a and 1b for system 2 are contained in and on the boundary of the region R' , where $\delta < \min[x_e, y_e]$ is a fixed number, and \tilde{x} is chosen so that R' will have an interior.

where $x_e = (a_2 / \lambda_2)$, $y_e = (a_1 / \lambda_1)$, (a_1 , a_2 , λ_1 , $\lambda_2 > 0$), c is a constant, and φ is the continuously differentiable function

$$\begin{aligned} \varphi(u) &= \left(1 - \frac{u^2}{\delta^2}\right)^2 \text{ when } |u| < \delta \\ \varphi(u) &= 0 \text{ when } |u| \geq \delta \end{aligned}$$

for the fixed positive number $\delta < \min[x_e, y_e]$. Define

$$\begin{aligned} V(x,y) &= \lambda_2(x - x_e) - a_2 \log\left(\frac{x}{x_e}\right) \\ &\quad + \lambda_1(y - y_e) - a_1 \log\left(\frac{y}{y_e}\right) \end{aligned}$$

and choose \tilde{x} to satisfy the two conditions $\tilde{x} > x_e + \delta$ and

$$V(\tilde{x}, y_e) > V(x_e - \delta, y_e - \delta)$$

This completes the description of system 2.

It is a straightforward matter to verify that system 2 satisfies our hypotheses when $|c|$ is sufficiently small. The equilibrium point (x_e, y_e) is stable if $c < 0$ and unstable if $c > 0$. On studying the behavior of (dV/dt) along solutions of system 2, one can show that, if $c \neq 0$, all periodic solutions of system 2 are contained in a closed annular region R' . The outer boundary of R' is the solution of the Lotka-Volterra system (4),

$$\frac{dx}{dt} = x(a_1 - \lambda_1 y) \quad (3a)$$

$$\frac{dy}{dt} = y(\lambda_2 x - a_2) \quad (3b)$$

which is tangent to the line $x = \tilde{x}$; the inner boundary of R' is the solution of system 3 which passes through the point $(x_e - \delta, y_e - \delta)$ (see Fig. 1). Since in R' systems 2 and 3 coincide, and since all the solutions of system 3 are periodic (4) (hence none are stable or unstable), it follows that all periodic

solutions of system 2 are neither stable nor unstable.

We remark, finally, that our system 2 need not be of any biological significance. The system was chosen merely to show that the dynamical Eqs. 1a and 1b can admit a continuum of neutrally stable periodic solutions when our hypotheses are the only requirements.

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References and Notes

1. R. M. May, *Science* **177**, 900 (1972).
2. A. N. Kolmogorov, *Giorn. Inst. Ital. Attuari* **14**, 1 (1936).
3. By "stability" of a periodic solution, May (1) and we mean asymptotic orbital stability.
4. N. S. Goel, S. C. Maitra, E. W. Montroll, *Rev. Mod. Phys.* **43**, 231 (1971).

24 November 1972; revised 20 February 1973

It is true that I could have been more meticulous, particularly in my footnote 17 in (1), and that, in addition to stable equilibrium points and stable limit cycles, there can be exceptional classes of (structurally unstable) neutrally stable periodic solutions. Although undoubtedly of some pedagogic and mathematical interest, such special neutrally stable periodic solutions are unlikely to be of biological significance. Albrecht *et al.* themselves make this point, and indeed their example is constructed with nonanalytic functions, whose higher derivatives are discontinuous.

The central fact remains that essentially all the explicit one predator-one prey models that have actually been propounded in the biological literature exhibit either stable equilibrium point or stable limit cycle behavior as the biological parameters are varied. This is the result sketched in my report (1), and it has subsequently been developed in detail, with a variety of examples (2). The remark that phenomena with stable limit cycles are likely to be pervasive in natural predator-prey systems [and in many other contexts (3)] is unaffected by the comments of Albrecht *et al.*

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References

1. R. M. May, *Science* **177**, 900 (1972).
 2. ———, *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, N.J., 1973), pp. 79-94.
 3. ———, *ibid.*, chap. 4.
- 20 July 1973