confidently that "there is almost no gene flow in this species over gaps of as little as X meters. . . ." Does it seem likely that the current outbreak of the coral-eating starfish, *Acanthaster planci*, throughout the Pacific Ocean (*5*) is without genetic consequences? The potential evolutionary significance of intermittent gene flow associated with fluctuations of population size has been considered by Brown (*6*) in a paper which, although not cited by Ehrlich and Raven, offers an alternative explanation of "bipolarity."

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2. E. B. Ford, *Ecological Genetics* (Methuen, London, 1965), pp. 12–16. Whether gene flow actually occurred as a result of the expansion of the Cumberland colony of *E. aurinia* is problematical, but the potential was certainly present.
3. A. B. Klots, *Field Guide to the Butterflies* (Houghton Mifflin, Boston, 1951), p. 258.
4. See Annual Summary for 1968, *Lepid Soc. News* (15 April 1969), pp. 17–20.
5. J. H. Barnes, *Austral. Nat. Hist.* **15**, 257 (1966); *Smithson. Inst. Center for Short-lived Phenomena, Reports 532, 535, 563, 600, 617, 636, 687, 738* (1969).
6. W. L. Brown, Jr., *Quart. Rev. Biol.* **32**, 247 (1957).

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In the 10-year period during which we have observed three colonies of *Euphydryas editha* populations on Jasper Ridge, a number of "population explosions" have been observed (*1*). For instance, population in area C increased from roughly 70–90 to 1000–1200 individuals (1962–1968), and in area G from 130–150 to 3000–5000 (1960–1965). No increase in "mixing" occurred; indeed, our data show that interpopulation exchange of individuals decreased. There is no reason to believe that the "explosion" of *E. aurinia* discussed by Ford and Ford (*2*) resulted in substantially increased interpopulation mixing or gene flow.

Whatever the degree of exchange of individuals, gene flow, to be of evolutionary importance, must constitute a source of novel genetic information that is incorporated into the recipient population. Whether or not such incorporation will occur will depend largely on the selective situation. If a great deal of individual movement occurs in a species which depends largely on phenotypic adjustment to different local conditions, there will not be important gene flow because immigrant individuals will be genetically similar to those already in residence. In species where adaptation is largely genetic the moving genes usually will be promptly selected out of the population, and gene flow will not have been significant. It seems to us that the greatest evolutionary potential for gene flow might occur in the introduction of entire coadapted gene complexes into a population, complexes which are somewhat less likely than mutations to have been previously "tried" by the recipient population.

If the Stanford group had been studying *Euphyes bimacula* for 10 years, we would be able to make reasonably confident statements about gene flow among the populations investigated, a subject on which the lepidopterists' reports (*3*) of "veritable outbreaks in places as far apart as Maine and Pennsylvania" casts no light whatsoever.

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Many genecologists will welcome the article by Ehrlich and Raven (*1*) that points out the importance of studying natural selection as a stabilizing force in evolution as well as an agency producing divergence. They will surely praise the authors' emphatic view that such studies must be conducted at the population level rather than by treating species as "evolutionary units." Their article is unexceptionable except where they suggest that gene flow within and between flowering plant populations must be low because the usual pollen vectors are relatively inefficient in spreading grains around. But pollen dispersal is not the only way in which gene flow can be achieved with plants; seed dispersal is often as effective and may be even more effective. Until we can be more quantitative in our estimates of gene flow through seed dispersal (including long-distance seed dispersal) we would be in error to ignore it.

However, I was delighted to read the comment that "The most basic forces involved in the differentiation of populations may be antagonistic selective strategies, one for close 'tracking' of the environment and one for maintaining 'coadapted' genetic combinations—combinations which have high average fitness in environments which are inevitably variable through time." Several of us (*2*) have put forward similar views (with evidence) and I am assembling evidence for their substantiation in a number of other plant genera (*3*).

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Bed Forms in Base-Surge Deposits: Lunar Implications

Fisher and Waters (*1*) have described bed forms of sedimentary deposits which could reasonably have been formed by a base-surge mechanism near meteor craters and volcanoes. Because some telescopically observed surface features of the moon show surface patterns similar to base-surge deposits on earth, and because base surges are observed for large explosive events on earth, they conclude that base surges may have been important in dispersing and depositing debris on the lunar surface, irrespective of the kind of cratering mechanisms.

Because base surge is an important phenomenon in the distribution of radioactivity from shallow water and shallowly buried nuclear blasts, it has received intensive study by physicists interested in nuclear weapons effects. Both theoretical and model studies (*2*) have shown that the base surge is a two-fluid gravity flow. Water droplets or dust particles in the stem of the familiar mushroom, when they start to fall, entrain the air in the hollow stem. The laden air then acts as a fluid with a density on the order of 1.5 times that of the surrounding atmosphere. At the base of the falling column, the vertical flow of the more dense aerosol is changed by the surface of the earth to a horizontal flow. The falling particles then must travel across streamlines of flow in order to be deposited on the earth's surface. Calculations of the "stopping distance" at which a particle will be brought to rest by viscous forces in still air show that an insignificant number of the particles will impact the earth while most of them will form a radially expanding base surge along the surface of the earth.

In the absence of an atmosphere, particles lofted by an explosive process will not entrain air. Even if the explosive process is of volcanic origin with enough gas emitted to form some sort of aerosol, a base surge will not form without a surrounding atmosphere to produce the two-fluid effect. The comparison is similar to that of a landslide, in which the density of the "moving fluid" is much greater than that of the surrounding fluid of the atmosphere, with an underwater landslide or turbidity current which may move for some hundreds of kilometers across a very nearly horizontal surface in the ocean. Base surges of the type described by Fisher and Waters cannot exist in the absence of an atmosphere and therefore cannot be considered a factor in lunar sedimentation at the present time. The base-surge mechanism could possibly have been of importance if in the past the moon had a significant atmosphere.

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3 November 1969

According to Grine (*1*), who cites a paper by G. A. Young (*2*), a base surge develops when water droplets or dust particles within a vertical explosion column start to fall and entrain air on the way down; at the base of the falling column, the aerosol is changed by the surface of the earth to a horizontal flow. It was concluded by Young (*3*), in a later paper, however, that the base surge forms from the crest of a large solitary wave which develops by gases expanding from the center of explosion. The top of this wave breaks and feeds the base surge. In Young's (*3*) study of the base surge which developed during the 1946 Bikini underwater atomic explosion, he noted that the main base surge appeared before the outside of the central column had started to fall. Similar early appearance of the base surge has been photographed at Capelinhos Volcano (*4*), and at the Sedan nuclear explosion (*5*).

The pertinent point is whether a base surge could develop and flow in the absence of an atmosphere. We maintain that it is probable because large impacting meteorites could produce large quantities of vapor.

Upon impact, a large volume of particulate matter would be entrained in gas—a mass which doubtless would be highly turbulent. If a large solitary wave were formed, this mass would then move laterally. How far such a flow could move would depend upon its size, the pull of gravity, the internal forces of friction ("viscosity"), and other factors. The particles within the mass could move within the newly created and internal gaseous "atmosphere," and could be deposited and buried without ever experiencing the effects of travel within a vacuum. Additionally, the leading edge and outer surfaces of the flow, in the absence of an external atmosphere, would move without experiencing inhibiting frictional drag. Thus, it seems reasonable to assume that under 1/6 gravity, such a mass would not only move, but perhaps could move farther than a cloud of comparable size on earth.

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9 January 1970

Bark Beetle Pheromones

Although we have attempted to clarify some issues related to research on bark beetle pheromones in other reviews (*1*, *2*), Pitman's recent comment (*3*) deserves reply.

The methodology used by Pitman and his colleagues at the Boyce Thompson Institute is so different from ours that direct comparison of results is difficult. We have attempted systematically to isolate and identify the compounds in bark beetle frass that are attractants. Chemical fractionation of frass is monitored with an olfactometer where beetles exhibit an upwind taxis in response to attractants. After such sequential fractionation, the active compounds are isolated in pure form, identified, and synthesized. The synthetic compounds are then exposed in olfactometers under field conditions, in order to determine their effectiveness in attracting beetles in flight. The group at Boyce Thompson has been attempting to identify the major volatile compounds in hindguts and then to determine if they are attractants in the field. The compounds are tested alone or in combination with gross oleoresin from the host tree or with the major known host monoterpenes.

Their identification of pheromones has been derivative (*2*). We isolated and identified both *exo*- and *endo*-brevicomin from the frass of *Dendroctonus brevicomis* females (*4*). In the course of the isolation, we found that a hydrocarbon fraction strongly synergized the activity of brevicomin. One of these synergistic compounds was identified as myrcene (*5*). In the field *exo*-brevicomin was attractive, and, as in the laboratory, the mixture of it and myrcene was the most attractive (*6*). After our announcement of brevicomin (*7*), Kinzer, working with the group from Boyce Thompson, isolated a very close analog of brevicomin from the hindgut of *D. brevicomis* males (*8*). (Brevicomin is a bicyclic ketal with a methyl and an ethyl substituent; Kinzer's compound is a bicyclic ketal with two methyl substituents.) No biological significance relative to *D. brevicomis* was ascribed to this compound by Kinzer, and no acknowledgment was made