Central American Sea-Level Canal: Possible Biological Effects

An opportunity for the greatest biological experiment in man's history may not be exploited.

Ira Rubinoff

Balboa discovered the Pacific Ocean 455 years ago, after a brief journey across the Isthmus of Panama. The possibility of constructing an interoceanic canal in Central America was raised almost immediately. Preliminary studies ordered by Charles V were made before 1530, and in 1534 he ordered an investigation of the feasibility of using the Chagres River valley as a route (*1*). Nothing was done, but the idea remained of interest to the Spanish crown until the early 19th century when independence movements in the colonial empire generally reduced the importance of such a waterway to Spain. Since then, canal projects have been a matter of more or less serious preoccupation to Panama and other Central American republics, Colombia, England, France, and the United States (beginning in the administration of Jefferson).

Although alternative routes were considered from time to time through the centuries, the Chagres valley was selected by the first French Canal Company, the first organization actually to attempt construction. The Chagres valley also was adopted by their American successors. The Panama Canal, in which locks are used, was completed in 1914. It was a great success, but now it is becoming increasingly inadequate and probably will not be able to cope with either the increased number or the size of the ships which will attempt to use it in the future (*2*).

Thus, the need for a new canal is obvious, and a sea-level canal, without locks, would be the most desirable replacement. Many of the problems raised by the prospect of a sea-level canal are similar to those discussed 50 to 75 years ago. Will the cost of the project be justified in terms of benefits to shipping or to hemispheric defense? Can satisfactory diplomatic arrangements be made with the host country? The only new factor is the possibility of using nuclear cratering techniques, and the necessity for evaluating the consequences.

Since World War II, there have been a series of studies concerned with both the problems of converting the Panama Canal to sea level by conventional means and of finding alternative sea-level routes. An investigation authorized by the 79th Congress (1947) considered 30 different routes from the Isthmus of Tehuantepec in Mexico south and east to northwest Colombia. In 1960, a report by the president of the Panama Canal Company included five routes suitable for nuclear excavation (Tehuantepec, Mexico; Nicaragua–Costa Rica; San Blas and Sasardi Morti in Panama; and Atrato-Truando in Colombia) (Fig. 1).

In 1965, President Johnson established the Atlantic-Pacific Interoceanic Canal Study Commission whose members he authorized to call upon any department or agency of the executive branch for advice and assistance in collecting and evaluating technical data necessary to determine the feasibility of constructing a sea-level canal. In addition to engineering problems, pertinent political, military, and economic problems related to location, construction, and operation of a sea-level canal were to be analyzed. Extensive studies have been and are being carried out by the commission and its contractors. These include: engineering studies of problems such as flood control, sedimentation, and channel hydraulics; studies of radioactivity, ground shock, and air blast; as well as studies in other areas including meteorology, geology, navigation, and medicine. Bioenvironmental studies, exclusive of literature surveys, have been restricted to analyses of the dangers to human ingestion of organisms which may become contaminated with radionuclides. In the ocean, the cycling of radionuclides is particularly complicated. In inshore environments there is a continuous exchange between the sediments, bottom filter feeders, and free-swimming organisms. Most direct human contact with radionuclides would come from this system. In the open sea, radionuclides can be distributed over large areas by ocean currents and migratory organisms. However, the dangers involving larger geographical areas are somewhat offset by dilution effects.

The Major Problem

It might therefore be supposed that the problems inherent in a sea-level canal were known and that complete and thorough efforts were being made to provide the information necessary to assay all the possibly dangerous consequences. Unfortunately, this is not true. One major aspect of the situation has been almost completely ignored. There will be major biological effects of a sea-level canal regardless of the site selected or the methods of construction used.

At present, the lock canal appears to be quite effective as a barrier to the migration of marine organisms from one ocean to another (*3*). The crucial factor is not the physical interposition of locks but the fresh water of Gatun Lake between the locks. A few euryhaline fishes transit the lake occasionally, but only one species is known to have gone from one ocean to the other and established a breeding population there (*4*). Sessile invertebrates of various types can effect interoceanic invasion as fouling attached to the bottom of ships, and planktonic forms might possibly transit in ballast tanks, but they certainly have not colonized new areas on a major scale.

The proposed sea-level canal will be a different matter. It will remove the barrier and will permit intermingling of

The author is assistant director for marine biology at the Smithsonian Tropical Research Institute, Balboa, Canal Zone.

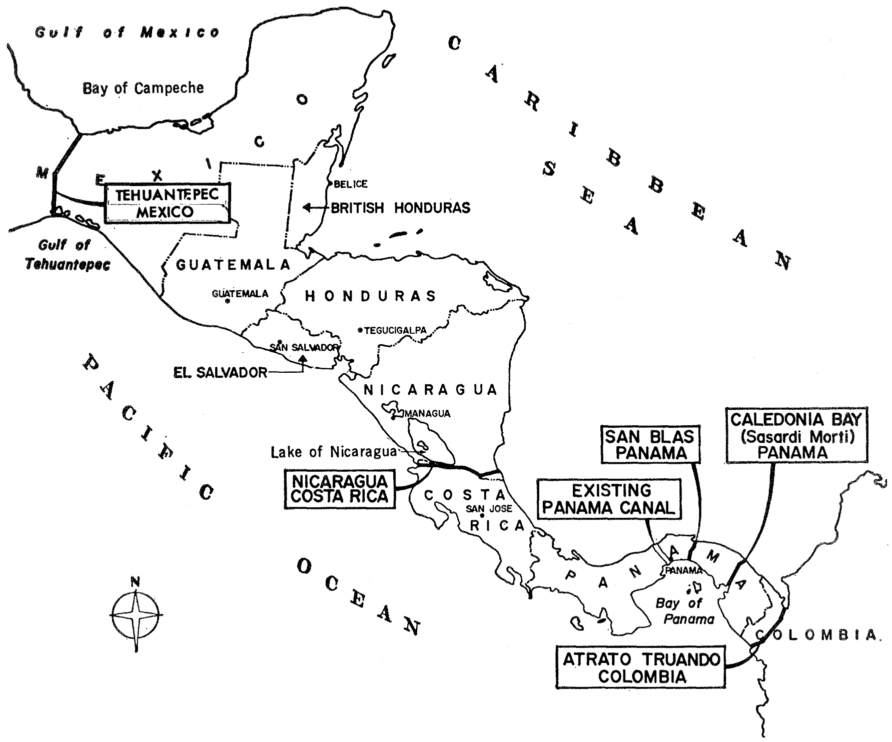

Fig. 1. Some possible sea-level canal routes in Central and South America.

large parts of the Atlantic and Pacific biotas. In effect, there will be a whole series of nearly simultaneous invasions and introductions of species into new areas.

The only other man-made connection of great bodies of water is the Suez Canal connecting the Mediterranean and Red seas. The situation of this sea-level canal is not similar to that planned for a Central American site. The Bitter Lakes, incorporated into the Suez Canal, represent a high-salinity barrier to migrations of most tropical organisms of the Red Sea and to most subtropical organisms of the Mediterranean. The salinity of the Bitter Lakes, however, has gradually decreased (from 68 to 45 per mille) since 1869, and the migrations of organisms through the canal has been facilitated. Over 150 species occurring in the eastern Mediterranean originated in the Red Sea, and possibly two species are reverse immigrants. Some of these immigrants are economically important, and nine of the commercially exploited species of the Mediterranean coast of Israel are of Red Sea origin (*5*).

The history of introductions and invasions of plants and animals as a result of human interference has, as often as not, been fraught with disaster. Elton (*6*) says these introductions frequently lead to ecological explosions. That is, "an enormous increase in numbers of some kind of living organism—it may be an infectious virus like influenza, or a bacterium like bubonic plague, or a fungus like that of the potato disease, a green plant like the prickly pear, or an animal like the grey squirrel. I use the word 'explosion' deliberately, because it means the bursting out from control of forces that were previously held in restraint by other forces."

One of the most notorious examples (and most pertinent in this connection) of an environmental manipulation leading to a population explosion is the construction of the Welland Canal which permitted the sea lamprey to invade the western Great Lakes. It took approximately 100 years for the population explosion of the sea lampreys to occur, but when it did, it resulted in the decimation of the whitefish and lake trout fisheries. In the last 12 years the United States and Canada have contributed approximately $16 million for control measures and research of this problem (*7*). This figure does not include the millions lost by the fishing industry of this region or the contributions of the various state conservation and fishery research programs. Other examples of outbreaks of populations after introductions into the United States include: Japanese beetles (*Popillia japonica*); European gypsy moth (*Porthetria dispar*); South American fire ant (*Solenopsis saevissima*); and the Asiatic chestnut blight (*Endothia parasitica*), the latter completely eliminating the domestic chestnut trees (*8*).

Spectacular as some of these cases may have been, they are minor by comparison with what would be expected to result from the construction of a sea-level canal in Central America. The mutual invasions of Atlantic and Pacific organisms should be much more extensive, numerous, and rapid, and their ultimate consequences should be quite incommensurable with any biological changes ever recorded before.

History of the Isthmus and Environments

The precise date at which an uninterrupted isthmian landbridge emerged is not known. The isthmus while acting as a barrier to marine organisms has been a landbridge for the exchange of North and South American terrestrial fauna. This landbridge had certainly been in full operation throughout the Pleistocene (*9*), and the water gap probably was finally closed during the latter part of the Pliocene (*10*). This would mean that the eastern Pacific and western Atlantic marine populations have remained separated for at least 3 or 4 million years.

Because the interruption of the Atlantic and Pacific oceans in this area has been geologically recent, there are still many similar forms of vertebrates and invertebrates on the opposite coasts. In a few cases, these Atlantic and Pacific populations are indistinguishable, although most have evolved minor differences and some have changed profoundly since they became isolated by the rise of the isthmus. The more closely related allopatric species have been referred to by a number of designations including: "species pairs," "geminate species," and "amphi-American species" (*11*).

Such divergence as has occurred may be largely a result of adaptations to the dissimilar environments on the respective coasts. The waters along the Atlantic and Pacific coasts of the isthmus at certain times of the year differ greatly in temperature, salinity, transparency, degree of tidal fluctuation, and, most important, in the biota which they support.

The Atlantic coast consists of a series of sandy beaches and extensive mangrove swamps, interspaced with and overlapping long fringing coral reefs.

The tops of these reefs are frequently exposed at low tides. There is some exposure of volcanic rocks along the Atlantic coast, although it does not constitute nearly as extensive an inshore habitat as it does along the Pacific coast.

The most outstanding topographical feature of the Pacific coast is the presence of numerous lava flows extending into the Pacific at frequent intervals along the coast. In some areas, these lava flows extend into the Pacific for almost a mile and many tide pools are formed in the irregular surfaces. The shoreline between these flows consists of muddy or sandy beaches and mangrove swamps.

The Atlantic water conditions adjacent to the isthmus are relatively constant. The differences between maximum and minimum recorded water temperatures at Cristobal are only about 6°C (Fig. 2). The difference between maximum and minimum tide at Cristobal is well under 0.5 meter, with the mean daily range averaging less than 0.3 meter (Fig. 3). The tides here are mixed diurnal, varying from two lows and two highs each day to one low or one high with intermediate conditions also being exhibited. The rainfall along the Atlantic slope is greater than along the Pacific slope, and the temporary dilution of the surface waters at the height of the rainy season along the Caribbean may be higher than that along the Pacific coast.

Compared to the relatively constant conditions found along the Atlantic coast, the Pacific waters are variable. The differences between recorded maximum and minimum temperatures at Balboa are as much as 18°C and the tidal amplitude in a single day can exceed 6 meters. From January through April (occasionally including periods of December and May) the Gulf of Panama is influenced by strong northeast trade winds. These winds drive the upper water mass offshore and produce upwellings of water from below 100 meters which is colder, more saline, and richer in nutrients than the water it replaces (*12*).

A striking contrast between the Atlantic and Pacific coasts is provided by the absence of coral reefs and a sparsity of attached algae along the Pacific mainland. This absence of coral reefs in the eastern Pacific is attributed to the periodic cold upwellings which frequently approach the lower physiological limit ascribed to reef corals. Other conditions, such as the lack of transparency of the water column and the prolonged desiccation due to the great tidal amplitude, undoubtedly also contribute to the general hostility of this region for corals. The turbidity of the water during flood tides may interfere with light transmission enough to inhibit photosynthesis in adherent algae as well as in coralline commensals.

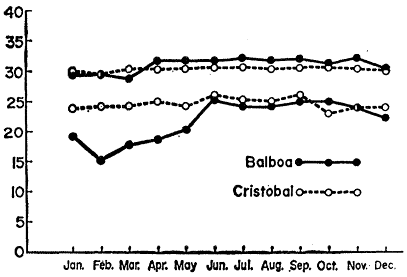

Fig. 2. Maximum and minimum sea-surface temperatures recorded at Balboa (Pacific) and Cristobal (Atlantic) 1907–1963. [Compiled from data collected by the Panama Canal Company, Meteorological and Hydrographic Branch.]

Possible Consequences

The possible general biological effects have been mentioned above. It may be useful, however, to consider some of the possible effects in more specific detail.

Theoretically, the results of sudden mixing of two formerly isolated populations can be predicted according to well-known genetic and ecological principles (*13*). Thus, for example, the potential for interbreeding between the newly intermixing populations depends upon whether or not they have diverged genetically during their isolation in ways that made them reproductively incompatible. Isolating mechanisms can be inherent in populations that have not diverged morphologically or may be absent in isolated populations that have diverged morphologically. However, the levels of morphological divergence and isolating mechanisms are usually correlated.

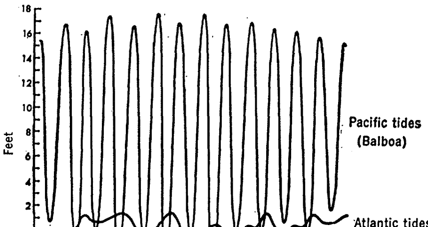

Fig. 3. Comparison of Balboa (Pacific) and Cristobal (Atlantic) tides, 11 to 17 April 1968 (1 foot ~ 0.3 meter). [Drawn from data in tide tables compiled by Coast and Geodetic Survey, U.S. Department of Commerce (1968)]

Not all allopatric populations have necessarily completed speciation, and it is expected that some of these populations might successfully fuse if the geographical barrier were removed. Depending upon the level of reproductive isolating mechanisms that have been evolved in allopatry, the effects of populations coming into contact with one another may be classified into the following not necessarily exclusive categories. (i) If during the period of allopatry no isolating mechanisms were developed, the populations may freely interbreed, producing a viable hybrid swarm. This swarm may eventually include the complete range of variability of both parental populations, or it may be limited to a narrow hybrid belt. The extent of such a hybrid belt will be determined by the ability of the hybrids to adapt ecologically to the geographical ranges of both parental populations. (ii) The newly sympatric populations may freely interbreed but if their genetic constitutions are not sufficiently similar (because of chromosomal rearrangements such as fusions or inversions) then swarms containing adaptively inferior individuals may result because of meiotic malorientations (*14*), and these could lead to the extinction of both populations. (iii) If the development of reproductive isolating mechanisms between two populations was begun but not completed in isolation, then occasional matings between individuals of the populations may be expected. These matings may be sterile, or the progeny may be inviable or sterile. In this case, those individuals whose behavior insures their mating only with others of their kind will be reproductively more successful, and isolating mechanisms will become more prevalent throughout the population. Selection will act to improve efficiency of some of the isolating mechanisms so that the two populations continue to remain separate. If, however, the occasional crossings between two populations do not produce adaptively inferior progeny, the two populations may react as in the first category, but somewhat more slowly. (iv) If the isolated populations have completed speciation before they mingle, they may coexist without interbreeding for part or all of their ranges, or competition between the two forms may cause replacement or extinction of one species by the other.

From the various degrees of divergence exhibited by the amphi-American species of shore fishes we have studied, one would expect that different groups will behave in all the ways enumerated above. Our laboratory is examining the degree of genetic isolation achieved in various groups of inshore fishes. Studies with two groups of Atlantic and Pacific marine gobies (*Bathygobius* and *Lophogobius*) indicate that many allopatric species are still interfertile and are not reproductively isolated at the gametic level. Experiments designed to test whether ethological isolating mechanisms have evolved demonstrated that allopatric species of these genera are reluctant to interbreed in "no-choice" mating experiments. This result was unexpected since other investigators have frequently been able to break down behavioral isolation between various related species by performing mating experiments with unbalanced sex ratios or by completely eliminating any choice of conspecific mates. We discovered that although it was difficult to induce heterospecific spawnings in experiments with one male of one species with one female of another (conspecific controls in adjacent aquariums were breeding regularly), such spawnings could be achieved if five or six males of one species were placed with five or six females of another. Some sort of social facilitation seems to be operating, and presumably a greater level of stimulation is necessary for successful heterospecific courtship and mating. Groups of individuals are the normal condition —the type of situation to be expected when a sea-level canal is completed. Whether or not there is a quantitative level of discrimination when both conspecific and heterospecific mates are available in equal numbers can be determined by "choice" experiments. At the same time, the relative viability and fertility of hybrids formed by heterospecific spawnings in the above groups (*15*) should be studied.

The principal ecological effects involve competition for different resources; for example, food, space to live and breed, and so forth. Interference may be direct—by the activities of one species against another—or indirect—through the influence of parasites or diseases of one species upon the other. We can anticipate that certain extant species will enlarge their niches owing to the removal of a competitor or some other species whose presence was restricting.

The construction of a sea-level canal may also change the physical environments on the respective coasts. It is conceivable, for instance, that a layer of warm Caribbean water could be spread through many miles in the eastern Pacific (*16*). The possible consequences of such developments are difficult to anticipate. At the very least, the resident populations and the new immigrants will have to make rapid adaptations. The influx of new organisms could upset the balance of populations, and certainly would change the nature of the selection to which organisms were subjected; we can expect an increase in turnover, the process of extinction of some species and their replacement by others. The population dynamics of some commercially important species may be disrupted by these changes.

Physical changes will probably have only local influence, their extent depending upon the volume of interoceanic flow and on the accompanying differentials in temperature, salinity, and silt. Biological results, by contrast, may have chain effects influencing the ecology of areas thousands of miles from the canal site.

Furthermore, the extinction occurring as a result of the mixing of the two biotas may involve forms that have either not been described yet or are still very rare in collections. Their disappearance before being studied would be a great loss to scientific knowledge and would effectively remove a potentially important historical base for biological oceanography of the future.

What Should Be Done?

The sea-level canal can provide a unique opportunity to advance our scientific understanding of evolutionary and ecological processes. In order to realize this potential it is necessary to treat the whole situation as an experiment in which case the necessary "control" is the pre-canal situation. If this is not thoroughly understood, then a large part of the contribution to knowledge that this engineering feat would afford will be lost forever.

Several types of biological studies should precede the construction of a sea-level canal if we are to have any hope of predicting the general consequences with any degree of adequate accuracy. A committee containing various marine systematists, ecologists, oceanographers, and statisticians should be convened and charged with the specific responsibility of organizing and operating a long-term quantitative and qualitative survey of the Atlantic and Pacific Central American region. They should be concerned with describing what is there, with what abundance, and with what seasonal, annual, and long-term fluctuations in densities (*17*). This committee should also be responsible for the critical task of organizing and executing the postcanal monitoring of the regions to assay what the canal-related changes are.

Analytical and experimental work should be initiated in a number of key groups to establish how Atlantic and Pacific species may interact genetically, ecologically, and behaviorally. Tests should be made of relative physiological, pathological, and parasitological tolerances of representative groups. It is not an impossible task to place samples of related populations from the Atlantic and Pacific oceans together experimentally, to learn how they compete for elements such as substrate, food, nest sites, or to challenge species experimentally with one another's parasites, or to test their physiological tolerances to hydrographic conditions on the opposite coast. Studies such as these will put predictions of the possible effects of Atlantic and Pacific intermingling on a sound basis of scientific data.

Concluding Remarks

It is no longer possible to permit only regional considerations and private interest groups to effect changes of wide-ranging implications. John F. Kennedy remarked to the National Academy of Sciences in October 1963:

> . . . I would mention a problem which I know has greatly concerned many of you —that is, our responsibility to control the effects of our own scientific experimentation. . . . In the past the problem of conservation has been mainly the problem of inadvertent human destruction of natural resources. But science today has the power for the first time in history to undertake experiments with premeditation which can irreversibly alter our biological and physical environments on a global scale.
>
> The problem is difficult because it is hard to know in advance whether the cumulative effects of a particular experiment will help or harm mankind. . . .

The government has the clear responsibility to weigh the importance of large-scale experiments to the advance of knowledge or to national security against the possibility of adverse and destructive effects. The scientific community must assist the government in arriving at rational judgments and in interpreting the issues to the public (*18*).

The necessary support must be provided to conduct adequate studies of the biological effects of a sea-level canal. Modern science can identify significant processes, quantify the relations of many oceanographic complexities, and resolve them in predictable patterns.

I believe that a control commission for environmental manipulation should be established and that this commission should be given broad powers of approving, disapproving, or modifying all major alterations of the marine or terrestrial environments in the United States, or any place where United States government or private contractors might be active. This commission should be multidisciplinary, independent of any single government agency, bureau, university, or private research institution, and it should have adequate funding to support its own investigations (*19*). Such a commission should be in operation before a sea-level canal is built, and its decisions should be made with the benefit of comprehensive biological investigations.

References and Notes

1. D. A. Arosemena, *Documentary Diplomatic History of The Panama Canal* (Imprenta Nacional, Panama, R.P., 1961).
2. Atlantic-Pacific Interoceanic Canal Study Commission, *A Plan For Study of Engineering Feasibility of Alternate Sea-Level Canal Routes Connecting the Atlantic and Pacific Oceans* (Atlantic-Pacific Interoceanic Canal Study Commission, Washington, D.C., 1965), 61 pp.
3. S. F. Hildebrand, *Sci. Mon.* **44**, 242 (1937); *Zoologica* **24**, 15 (1939).
4. R. W. Rubinoff and I. Rubinoff, *Nature* **217**, 476 (1968).
5. A. Ben-Tuvia, *Copeia* **1966**, 254 (1966).
6. C. S. Elton, *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958), p. 15.
7. U.S. Fish and Wildlife Service, personal communication.
8. D. Pimental, *Science* **159**, 1432 (1968).
9. W. P. Woodring, *Proc. Amer. Phil. Soc.* **110**, 425 (1966).
10. J. J. Lloyd, in *Backbone of the Americas* (American Association of Petroleum Geologists, Tulsa, Okla., 1962), p. 88.
11. A. Günther, *Trans. Zool. Soc. London* **6**, 377 (1869); C. H. Gilbert and E. C. Starks, *Mem. Calif. Acad. Sci.* **4**, 1–304 (1904); S. Ekman, *Zoogeography of the Sea* (Sidgwick and Jackson, London, 1953), pp. 30–55.
12. W. S. Wooster, *Amer. Mus. Natur. Hist. Bull.* **118**, 119 (1959); M. B. Schaefer, Y. M. M. Bishop, G. V. Howard, *Bull. Inter-Amer. Trop. Tuna Comm.* **3**, 79 (1958); E. D. Forsbergh, *ibid.* **7**, 1 (1963); T. J. Smayda, *ibid.*, p. 191.
13. E. Mayr, *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, Mass., 1963), 797 pp.; I. Rubinoff, *Natur. Hist.* **74**, 69 (1965).
14. M. J. D. White, *Science* **159**, 1065 (1968).
15. I. Rubinoff and R. W. Rubinoff, in preparation.
16. C. O'D. Iselin, personal communication.
17. It is commonly believed that population fluctuations in tropical species are minimum, but this certainly is not true of reptiles (O. Sexton, in press); mammals and birds (M. Moynihan, personal communication); at least some groups of insects (R. Dressler, personal communication); and it is my impression that the fluctuations in marine fishes are at least as great as in land animals. It is important to recognize that population studies should begin at least 10 to 20 years before a canal is completed if normal long-term population fluctuations are to be mapped. Without this data a canal may be "blamed" for sudden reduction or disappearance of species which might just coincidentally be at a density nadir.
18. New York *Times* (23 October 1963), p. 24.
19. For a recent discussion of federal activities in environmenal control, see *Environmental Quality*, Hearings before the House Subcommittee on Science Research and Development, Jan.–Mar., 1968, Emilio Q. Daddario, chairman (U.S. Government Printing Office, Washington, D.C., 1968).

20. Based in part on research supported by NSF grant GB-3450 and grants from the Smithsonian Research Foundation. I thank W. Aron, S. Galler, P. Glynn, E. Mayr, R. Menzies, M. Moynihan, R. Rubinoff, N. Smith, R. Topp for criticizing the manuscript.

Heart Poisons in the Monarch Butterfly

Some aposematic butterflies obtain protection from cardenolides present in their food plants.

T. Reichstein, J. von Euw, J. A. Parsons, Miriam Rothschild

It was noted nearly a hundred years ago that butterflies of the subfamily Danainae were unpalatable to the majority of insectivorous birds (*1*), and this observation has frequently been confirmed (*2–6*), both in nature and in the laboratory. Some species, however, can apparently eat these butterflies with impunity. Swynnerton (*7*), who was the first to record vomiting in captive birds following the ingestion of *Danaus chrysippus* (L.) and *Amauris echeria lobengula* Sharpe, believed that *Crateropus* spp. (babblers) preferred this type of food (and other distasteful species such as blister beetles, *Mylabris* spp.); he also found that *Lophoceros melanoleucus* (Licht.) suffered little or no ill effects from eating danaids. One of us observed that *Kittacincla malabarica* (Gm.) ate *D. plexippus* without hesitation (*8, 9*) despite the fact that it usually regurgitated the insect immediately and then reswallowed it. When very hungry, many species of birds (*2*) will eat one or even two specimens of danaids, and shrikes (*Lanius*) have been seen impaling them on thorns in their food stores.

Slater (*10*) in 1887 suggested that gaily colored caterpillars were protected by the poisonous substances they obtained from the plants they feed on. Our observations suggest that this surmise is correct in the case of *Danaus*. Slater's choice of examples was somewhat unfortunate as he included in his list species which, although brightly colored, are essentially cryptic in habit. He thus bracketed the larvae of *Danaus* and of the oleander hawkmoth [*Deilephila nerii* (L.)].

Haase (*11*) was also of the opinion that warningly colored species (that is, aposematic species) obtained their deterrent qualities directly from the foliage consumed by their larvae. Poulton (*12*), with more insight, agreed that this might well be the case for those groups which specialize in feeding on one group of toxic plants, all closely related (examples are the dan-

Professor Reichstein is professor of organic chemistry at the University of Basel, Basel, Switzerland; Dr. von Euw is Professor Reichstein's assistant in the department of organic chemistry, University of Basel; Dr. Parsons is pharmacologist at the National Institute for Medical Research, Mill Hill, London; The Hon. Miriam Rothschild is an amateur naturalist, of Ashton, Peterborough, England.