ILLINOIS
atural History Survey
BULLETIN

# 125 Years of Biological Research 1858–1983: A Symposium

STATE OF ILLINOIS
DEPARTMENT OF ENERGY AND NATURAL RESOURCES

NATURAL HISTORY SURVEY DIVISION
CHAMPAIGN, ILLINOIS

VOLUME 33, ARTICLE 3
SEPTEMBER 1985

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(Continued to Back Cover)

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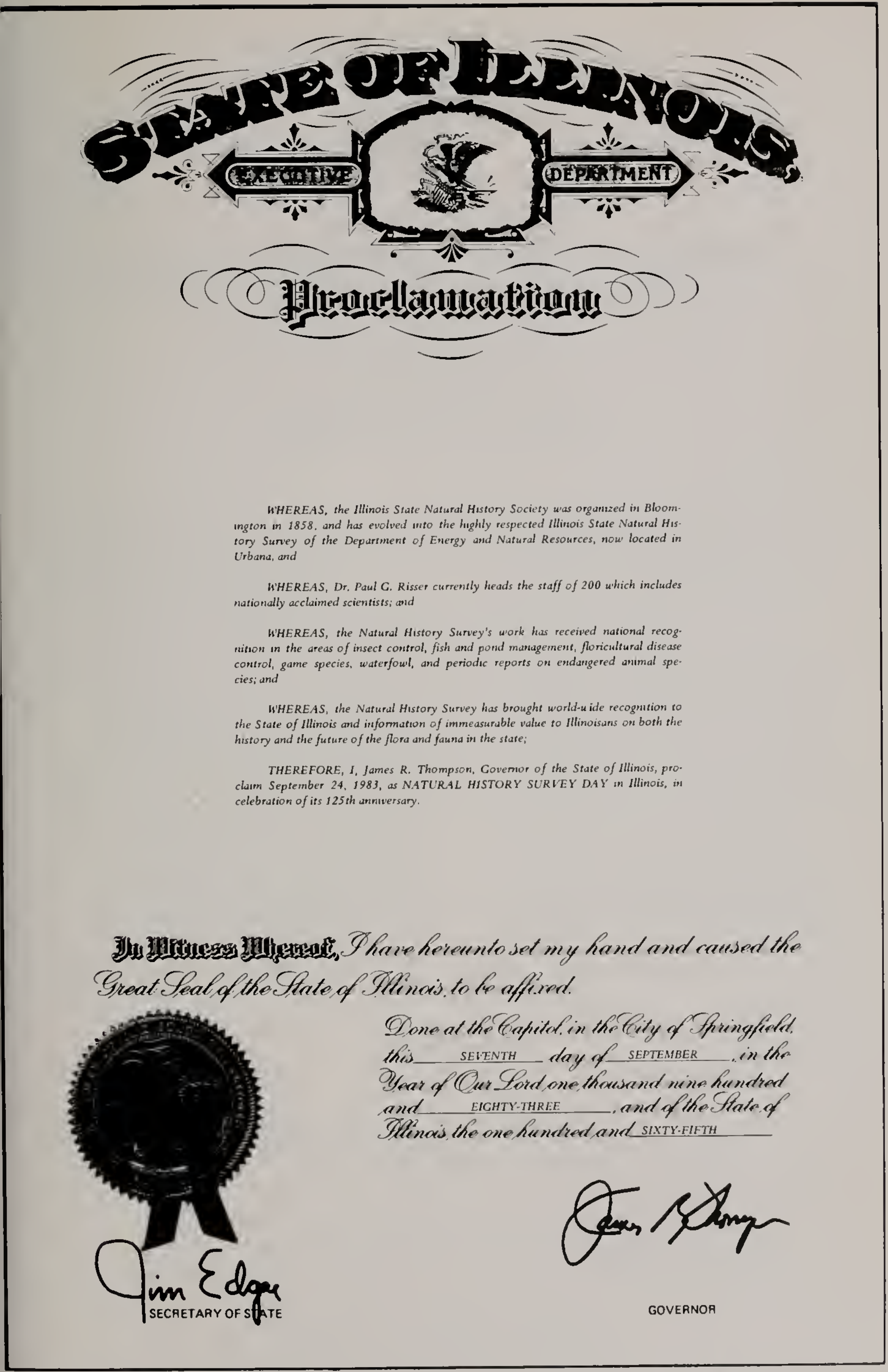

# STATE OF ILLINOIS

EXECUTIVE DEPARTMENT

## Proclamation

*WHEREAS, the Illinois State Natural History Society was organized in Bloomington in 1858, and has evolved into the highly respected Illinois State Natural History Survey of the Department of Energy and Natural Resources, now located in Urbana, and*

*WHEREAS, Dr. Paul G. Risser currently heads the staff of 200 which includes nationally acclaimed scientists; and*

*WHEREAS, the Natural History Survey's work has received national recognition in the areas of insect control, fish and pond management, floricultural disease control, game species, waterfowl, and periodic reports on endangered animal species; and*

*WHEREAS, the Natural History Survey has brought world-wide recognition to the State of Illinois and information of immeasurable value to Illinoisans on both the history and the future of the flora and fauna in the state;*

*THEREFORE, I, James R. Thompson, Governor of the State of Illinois, proclaim September 24, 1983, as NATURAL HISTORY SURVEY DAY in Illinois, in celebration of its 125th anniversary.*

**In Witness Whereof,** *I have hereunto set my hand and caused the Great Seal of the State of Illinois to be affixed.*

*Done at the Capitol, in the City of Springfield, this* SEVENTH *day of* SEPTEMBER*, in the Year of Our Lord one thousand nine hundred and* EIGHTY-THREE*, and of the State of Illinois the one hundred and* SIXTY-FIFTH

Jim Edgar
SECRETARY OF STATE

GOVERNOR

Frontispiece. – Governor James R. Thompson's proclamation, declaring 24 September 1983 Illinois Natural History Survey Day.

# ILLINOIS NATURAL HISTORY SURVEY
## 125TH ANNIVERSARY CELEBRATION

### SYMPOSIUM

274 Medical Sciences Building
University of Illinois, Urbana, IL
(Open to the public – no charge)

**Morning Session**

Moderator – Dr. F. A. Bazzaz, Head
Department of Plant Biology
University of Illinois, U-C

9:00 Opening. Dr. P. G. Risser, Chief, INHS

9:05 A host plant is more than its chemistry. Dr. D. H. Janzen, Professor of Biology, University of Pennsylvania, Philadelphia

9:55 Plant kairomones and insect pest control. Dr. R. L. Metcalf, Professor of Biology and Research Professor of Entomology, University of Illinois, Urbana-Champaign, and Principal Scientist, INHS

10:25 Break

10:35 Early contributions of insect toxicology to the evolution of environmental toxicology. Dr. A. S. Felsot, Associate Entomologist, Section of Economic Entomology, INHS

11:05 Biotic and abiotic stresses as primary and predisposing factors affecting Illinois trees. Drs. D. F. Schoeneweiss, D. Neely, and E. B. Himelick, Plant Pathologists, Section of Botany and Plant Pathology, INHS

11:35 Summary. Dr. C. E. Eastman, Associate Entomologist, and Dr. M. Kogan, Entomologist, Section of Economic Entomology, INHS

11:45 Adjournment

### LUNCHEON

12:00–1:45 PM
Illini Union Rooms B and C
University of Illinois, Urbana, IL
(Open to the public by reservation)

Recognition of
Friends of the Illinois Natural History Survey

Luncheon Address
"Long-term Biological Research in a Rapidly Changing Environment"
by
Dr. Lorin I. Nevling, Jr., Director
Field Museum of Natural History
Chicago, IL

## Afternoon Session

Moderator – Dr. J. E. King, Head
Scientific Sections
Illinois State Museum
Springfield, IL

2:15 Opening. Dr. P. G. Risser, Chief, INHS

2:20 Lake Tahoe: a microcosm for the study of change. Dr. C. R. Goldman, Director of the Lake Tahoe Research Group, Division of Environmental Studies, University of California, Davis

3:05 A comparison of the embryonic development of northern, Florida, and reciprocal $F_1$ hybrid largemouth bass in different thermal environments. Dr. D. P. Philipp, Associate Aquatic Biologist, and Ms. C. Kaminski, Junior Technical Assistant, Section of Aquatic Biology, INHS, and Dr. G. S. Whitt, Professor of Genetics and Development, University of Illinois, Urbana-Champaign, and Research Affiliate, INHS

3:35 Break

3:45 Evolution of reproductive behavior in percid fishes. Dr. L. M. Page, Ichthyologist, Section of Faunistic Surveys and Insect Identification, INHS

4:15 Wind drift and migration of thrushes: a telemetry study. Mr. W. W. Cochran, Associate Wildlife Specialist, Section of Wildlife Research, INHS, and Mr. C. G. Kjos, Fish and Wildlife Biologist, U.S. Fish and Wildlife Service, Department of the Interior, Fort Snelling, MN

4:45 Summary. Dr. J. R. Karr, Professor of Ecology, Ethology, and Evolution, University of Illinois, Urbana-Champaign

4:55 Adjournment

# CONTENTS

LUNCHEON ADDRESS:

*This paper is published by authority of the State of Illinois and is a contribution from various staff members and guest speakers who made presentations on the occasion of the Survey's 125th anniversary year.*

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# ACKNOWLEDGMENTS

The Illinois Natural History Survey celebrated its 125th anniversary in 1983 by hosting a series of special events for its friends and staff. Two of them were the 125th Anniversary Symposium and Luncheon held on 24 September 1983 at Urbana, and the contents of this commemorative bulletin are based on the papers and summary comments presented at those two functions. The proclamation from Governor James R. Thompson, recognizing the importance of the Survey to the people of Illinois (Frontispiece), was read at the luncheon.

The papers contributed to the symposium were selected on the basis of recommendations solicited from the staffs of the Survey's research sections: Aquatic Biology, Botany and Plant Pathology, Economic Entomology, Faunistic Surveys and Insect Identification, and Wildlife Research. The papers presented by Survey staff members do not adequately reflect either past or present programs in toto, i.e., they are indicative, not definitive.

Each manuscript was subjected to rigorous review by the editorial committee and by at least 2 of 17 anonymous, non-Survey scientists. To these people and our colleagues, R. W. Larimore and W. G. Ruesink, comembers with us on the symposium program committee, we are grateful for quietly supporting us in the preparation of this publication. We also thank several members of the Survey's supportive staff, A. K. Adams, P. L. Duzan, R. J. Korb, L. L. Le Mere, S. H. McClellan, B. A. Nelson, S. J. Peratt, J. A. Sanders, E. L. Steger, B. P. Sweeney, and M. L. Williamson, who spared no effort in helping us to complete this volume. Finally, special thanks are due to F. A. Bazzaz, former Head, Department of Plant Biology, University of Illinois, Urbana-Champaign, and J. E. King, Head, Scientific Section, Illinois State Museum, Springfield, who served as moderators of the morning and afternoon symposium sessions, respectively.

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# An Introduction to the Symposium

Paul G. Risser

The Natural History Society of Illinois was proposed to the State Teacher's Association in December 1857 and was organized on 30 June 1858, thus beginning the 125 years celebrated by this symposium volume. The society subsequently became the Illinois State Laboratory of Natural History, which was combined with the State Entomologist's Office in 1917 and renamed the Illinois Natural History Survey. Early Illinois leadership recognized the need for a state agency committed to studying and understanding the living natural resources of Illinois. It is to the state's credit that the Illinois Natural History Survey has become during these past 125 years the largest and oldest organization of its kind in the nation.

A casual review might suggest that the Survey's early activities were largely surveys, that is, the careful cataloging and mapping of the flora and fauna of the state. Today's activities might easily be characterized as modern biology with emphases on the application of new technology and on studies addressing current environmental problems and the management of living natural resources. However, such casual inspection of the Survey's programs, past and present, would not identify and recognize the strengths which have enabled the organization to grow over the past twelve and a half decades.

Before the turn of the century, biologists from the State Laboratory of Natural History were indeed systematically sampling the state's terrestrial habitats as well as its rivers and streams. These early field investigations not only formed the basis for understanding these ecosystems and the natural histories of the organisms found therein, but also resulted in an informational record which is priceless in making comparisons with today's conditions. But further, Survey scientists developed biological-population sampling equipment and methodologies that have been adopted by biologists throughout the country. The resulting information was used to address such practical issues as increasing the production of fish populations in lakes; controlling agricultural pests, such as the chinch bug; and dealing with ticks and other wildlife problems. In addition, Survey scientists also began to develop a conceptual framework for these studies, a direction perhaps epitomized by the "lake-as-a-microcosm" concept of Stephen A. Forbes, the first Chief of the Survey.

The Illinois Natural History Survey retains these same basic ingredients. As described in the paper by L. M. Page in this volume, the Survey is conducting detailed life-history studies which provide information for understanding the evolutionary relationships among groups of species and, at the same time, result in recommendations about how to manage various species to ensure their perpetuation. The paper by D. F. Schoeneweiss, D. Neely, and E. B. Himelick clearly demonstrates a progression of approaches developed for controlling the diseases of urban and forest trees. These techniques depend upon a thorough knowledge of the life histories of the trees and their pests. The W. W. Cochran and C. G. Kjos paper discusses novel technology for investigating a fundamental biological phenomenon, migration of passerine birds. The paper by D. P. Philipp, C. Kaminski, and G.

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Dr. Paul G. Risser is Chief of the Illinois Natural History Survey and is a plant ecologist.

S. Whitt recounts the use of enzymological methods to describe differences among fish populations which otherwise would not have been discerned. Just as importantly, this information can now be used as the basis for recommendations about fish stocking programs in Illinois.

A. S. Felsot's paper on environmental toxicology considers the fate and behavior of agricultural pesticides in the environment, and this paper clearly emphasizes some rather unique characteristics of the Survey. Agricultural entomology has been an important component of the Illinois Natural History Survey ever since the Illinois State Laboratory of Natural History merged with the State Entomologist's Office. Controlling insect pests with chemicals is a widespread practice but is an approach viewed with skepticism by some of those attempting to preserve the living natural resources of the state. However, the compatibility of these potentially opposing viewpoints lies in the Survey's broad understanding of biological principles. In making recommendations about the control of agricultural pests, the Survey employs the concepts of integrated pest management, which specifies the minimum use of chemicals and the maximum use of information about the life history of both the host organism and the pest organism. Thus, the Survey is in the unique position of being able to address very practical problems with natural history data and ecological information.

The three guest authors in this volume presented papers which served to place the Survey's program in a national context. D. H. Janzen discusses current notions about the ways in which insects select and feed on plants. His point is that the customarily invoked mechanism based on the chemical constituents of the plant is focused too narrowly and that more natural situations will be explained by considering the natural history and evolutionary aspects of plant and insect interrelationships. In a more applied sense, R. L. Metcalf elaborates this thought with an elegant discussion of the evolutionary processes that led to the enormous array of secondary chemical compounds found in agricultural plants. C. R. Goldman reaffirms the holistic view of the lake ecosystem concept, using Lake Tahoe as the model. Here, again, his paper demonstrates the strength of understanding the natural history of the system and then managing the lake according to these biological principles.

As noted by L. I. Nevling, Jr., in his luncheon address, reflection on the past and future of the Illinois Natural History Survey indicates the unique attributes of the organization. The long-term purpose to understand the biology of the state and the dedication to do so are unusual commitments in this day when programs and objectives tend to be largely impulsive, ephemeral, and fragmented. The papers in this volume demonstrate the pervasive nature of the Survey's programs, which touch, directly or indirectly, every person in Illinois. The importance of the work, however, goes beyond the state's borders, since the state is a microcosm of the nation, and thus, the results of the program are applicable to all efforts to understand and manage biological resources in a changing world.

# A Host Plant Is More Than Its Chemistry

Daniel H. Janzen

Field naturalists frequently observe that the intensity of insect herbivory in a natural defoliation event is not spread uniformly over individual conspecific plants and may even vary within one plant crown. Until the early 1960's, the general explanation would have been that heterogeneity in physical conditions, carnivory, and/or the arrival of the herbivores generate such lack of uniformity. During the past 20 years, much research on the chemical defenses of plants has paved the way for the now commonplace concept that such heterogeneity of herbivory in a defoliation event may also be caused by heterogeneity in the nutrient or defense properties of plants or plant parts (e.g., Kogan 1977). Indeed, a number of studies have found this to be the case. For example, squirrels browse much more heavily on terpene-poor ponderosa pines than on their more terpene-rich conspecifics a few meters away (Farantinos et al. 1981). Panamanian forest insects browse young leaves more intensely than they do conspecific old ones, presumably because of the greater nutrient value and lesser toughness of the former (Coley 1982, 1983a, b). Chrysomelid beetles and Finnish caterpillars vary their feeding patterns in response to seasonal changes in host leaf chemistry (Hare 1983; Haukioja & Niemela 1979).

What I would like to do in this essay is to give the pendulum a push back toward a middle ground, reminding all of us (including me) that when a herbivore moves onto a host plant it gets the outside of the plant as well as what is inside. Such integrative studies are now beginning to appear in the literature (e.g., Abrahamson et al. 1983; Coley 1982, 1983a, b; Connor et al. 1983; Haukioja 1980; Heinrich & Collins 1983; Kareiva 1982; Lawton 1983; McClure 1983; Niemela et al. 1982; Price et al. 1980; Rausher & Papaj 1983; Schultz 1983; Schultz et al. 1982; Stanton 1982; Thompson 1983; Washburn & Cornell 1981; Wint 1983). I feel that the philosophy that generates them deserves maximum encouragement.

I have two practical reasons for attempting this leavening, though I am sure that the reader will think of others. First, one has only so much time and resource to expend on a given study of the intensity of herbivory, and there is a very real question of whether efforts should be focused on determining the (potential) internal plant properties that drive the system or on designing observations and experiments to reveal the external factors crashing down on the lowly caterpillar. Second, in attempting to understand the ecological and evolutionary distribution of herbivores among their host plants, it is easy to forget that what might be termed the carnivory regime and climate regime of a host plant individual or population are as much traits of a plant as is its chemical profile. Both of these regimes should count for much in whether and to what degree a plant or plant part is a suitable host. When we ask why a caterpillar feeds on only one particular host species, it may be as much that it is highly adapted to the predator risks and desiccation regimes of that plant as that it is adapted to the plant's internal chemistry. By the same token, when we ask what does a herbivorous generalist have to do to be a generalist, it may be as much that it has to be able to withstand the predation risks of living on various kinds of backgrounds (e.g., Heinrich & Collins

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Dr. Daniel H. Janzen is a Professor of Biology, University of Pennsylvania, Philadelphia.

1983) as to have the gut chemistry to tolerate various kinds of food (e.g., Ahmad 1983). Which ability came first may be lost in the decomposed pages of time.

I also have an apologetic reason for attempting to meld two sequential fashions. I think we erred in not recognizing two blended questions in the seminal essay that argued that since the herbivores did not eat the green world to the ground, or even down very much, they must be regulated by the carnivores (Hairston et al. 1960). Question one is why don't all the herbivores eat up all the plants? The answer that lay undiscussed by Hairston et al. (1960) is that most of the green world is inedible to any given species of herbivore. Also lying dormant was the derivative evolutionary question of why doesn't any given herbivore species evolve the ability to eat many kinds of plants? Question two is the real question in Hairston et al. (1960); why don't the herbivores that can readily and with impunity consume a species of host plant eat their host to oblivion? Every plant species has at least one herbivore that can eat it. To some degree a plant's herbivores do consume it, thereby leaving resources for other plant species, but to a large degree they do not, with the consequence that competition and the physical environment determine much of the structure of vegetation arrays. The very same carnivory and climatic regimes that prevent herbivores from eating their hosts to oblivion are also the traits of the potential new host that must be overcome when a herbivore evolutionarily moves to, or incorporates, a new host.

Nothing I have said is new, but I feel that the emphasis is different from that of contemporary ecology and evolutionary biology; this emphasis may be witnessed in two recent books on coevolution (Futuyma & Slatkin 1983; Nitecki 1983). Virtually no attention is given to this subject, while the coevolution of herbivores and plant chemistry plays a prominent role in examples and in generation of theory.

I have chosen briefly to describe four systems as illustrative case histories rather than to dwell on hypothetical structure. I do this because of my opinion that theory in evolutionary ecology is intrinsically prone to outrun description of what is actually happening out there.

## THE ARENA

The attitudes and examples in this essay derive from my experiences with the herbivore array of a lowland tropical forest, that of Santa Rosa National Park, in northwestern Guanacaste Province, Costa Rica (this site is described in detail in Janzen 1983a and in Boza & Mendoza 1981). This mosaic of deciduous forest, evergreen forest, semi-evergreen forest, and pastures regenerating to forests occupies about 11,000 ha from 0 to 350 m elevation between the Pan-American Highway and the Pacific Ocean. The area has a 5–6-month dry season (approximately December through April), and 1,000–2,000 mm of rain falls during the remainder of the year. Portions of the park were an operating cattle ranch from no later than 1710 to 1978. The vegetation contains at least 680 species broadleafed plants (at least 400 species of perennial woody plants) and supports at least 3,000 species of caterpillars plus several hundred species of other animals that eat living plant parts. There are checklists of plants (Janzen & Liesner 1980), birds (Stiles 1983), reptiles and amphibians (Scott et al. 1983), mammals (Wilson 1983), and butterflies (DeVries 1983) for the park. The plant distributions within this vegetation range from nearly monospecific stands of very large trees (e.g., 10–20-m-tall stands of *Quercus oleoides* Cham. and Schlecht., *Hymenaea courbaril* L., *Ateleia herbert-smithii* (Pittier) to highly mixed vegetation where as many as 200 species of woody plants may occur in 100 ha and adult conspecific crowns are usually separated by one to many allospecific crowns. At Santa Rosa, herbivory by caterpillars, the focus of this essay, is characteristically highly heterogeneous among years and among individuals, species, and age classes of plants (e.g., Janzen 1981).

## ANATOMY OF A DEFOLIATION EVENT

### The event

During the 1983 rainy season, a representative defoliation event occurred at Santa Rosa. The impact of the herbivores was highly heterogeneous. I briefly describe the ecology of this impact as an example of a pattern that could have been generated either by the heterogeneity of internal plant chemistry or by mortality factors external to the plant (or both). In fact, the pattern seems to have been generated by external factors and therefore provides an example for the introductory comments of this essay. It is described in more detail elsewhere (Janzen unpublished manuscript). While the study was conducted in a patch of Santa Rosa forest of approximately 2 km$^2$ (Bosque San Emilio, approximately 2 km northeast of the park administration area), the 11,000-ha park contains tens of square kilometers of this type of forest. Cursory examination of other forest patches showed that the events described here occurred at those sites as well.

### The first generation

From 28 May to 4 June 1983, when 50–90-year-old secondary successional deciduous forest at Santa Rosa was just beginning budbreak following the first significant rains of the rainy season, the forest was sprinkled with ovipositing *Aellopos titan* (Cram.). One or more of these small diurnal sphingid moths (Haber & Frankie 1983) could be seen by simply standing and looking through the forest for 5 minutes or less at any time during daylight hours. The moths darted among the shrubs and treelets at a height of about 1–3 m. They touched branchlets, twigs, and buds with legs and the tip of the abdomen. Upon encountering a plant of *Randia karstenii* Polak or *R. subcordata* (Stand.) Standley, the moth hesitated a moment longer and sometimes laid a single spherical pale green egg on the bud, newly expanding leaf, thorn, or twig it contacted (Fig. 1). It then flew to other branches of the same plant or, about equally frequently, off to neighboring plants. Both species of *Randia* were beginning budbreak; a few individuals were covered with a thin layer of newly expanding leaves, while others had only swelling buds. The outcome of this oviposition, by what must have been several thousand moths in the study area, was the deposition of tens of eggs to a thousand or more eggs on each *Randia* in the forest (of 214 plants briefly examined, all had some eggs).

For example, on 5 June, all or a major portion of the potential oviposition sites on 14, 1.5–5-m-tall *R. subcordata* were searched thoroughly for *A. titan* eggs. As many as 10 eggs had accumulated on some branch ends (Fig. 1C), but 1 or 2 per branch end or bud was more usual (Fig. 1A, B). The estimated or actual numbers of eggs on these plants ranged from 21 to 1,212, with an average of 197 (SD = 316). Smaller plants (0.7–1.4 m in height) had 1–19 eggs on them ($\bar{x}$ = 6.0, SD = 5.1, $n$ = 10). The small plants were not only shorter, but also had only one or a few stems and branchlets. While I did not count them, the numbers of *A. titan* eggs on the *R. karstenii* appeared to be about the same. Each hectare of this 2-km$^2$ patch of forest contains at least four individuals of these two *Randia* species that are 1.5 m or more in height, which allows a rough estimate of 800 oviposition plants carrying a minimum of about 160,000 *A. titan* eggs. If I assume that each female can lay 100 eggs, these eggs represent the oviposition by 1,600 moths.

Fig. 1. — (A) Egg of *Aellopos titan* laid on a spine of *Randia subcordata* at the time of budbreak. (B) Accumulated eggs of *A. titan* following multiple ovipositions over several days on *R. subcordata*. (C) Egg of *A. titan* laid on the underside of an expanding new leaf of *R. subcordata*. 30 May 1983, Santa Rosa National Park, Costa Rica.

From the outset, the number of eggs present on a given plant was the product of several processes. Even while females were ovipositing, eggs were being carried off by *Pseudomyrmex, Azteca, Crematogaster,* and other ants, picked off by warbler-sized and -shaped birds, and fed on by anthocorid bugs. The eggs hatched 5–6 days after oviposition; even as the first were hatching, more were still being laid. While minute parasitic Hymenoptera were observed ovipositing in the eggs in the field, no parasitoids were reared from a sample of 682 eggs collected from 24 different *R. subcordata* plants, and no parasitoids appeared when 100 of these eggs were reared to the adult stage.

The first-instar larvae are pale green, match well the color of the newly expanding *Randia* leaves, and wander widely through the foliage of the plant on which they hatch. They appear to be highly edible to the ants and birds mentioned above, reduviid bugs, *Polistes* wasps, other wasps, small spiders, and carabid beetles; all of these animals were observed to capture and eat them or carry them off on numerous occasions. By 4–7 June, tens to hundreds of first- or second-instar *A. titan* larvae could be found on any *Randia* more than 1 m tall, and some larvae were present even on plants as small as 30 cm in height. On all plants the larvae appeared to be healthy and were feeding heavily.

I was absent from the site 8–13 June, and upon my return, it was evident that the outbreak had developed to the extent that three levels of defoliation could be recognized among both species of *Randia*. There were plants with only a few larvae (1–10 per plant by quick inspection), plants with moderate numbers of larvae (10–30 per plant), and plants with hundreds of larvae. On all plants, the larvae appeared to be healthy and to have about the same size distribution. On 18–20 June, 49 *R. subcordata* plants were thoroughly searched at night for larvae. By searching at night with a strong flashlight, at least 99 percent of the larvae present on a plant were located. By these dates, virtually the entire population was in the ultimate (Fig. 2) or penultimate instar. A few larvae had already left their host plants to pupate or, if the host was defoliated, to search for more food. No larvae were on 43 percent of the plants, and all of these plants showed minor defoliation; however, there was enough defoliation to make it clear that some *A. titan* caterpillars had developed to moderate size on these plants before leaving or being preyed upon. The plants (33 percent) with 1–10 larvae had either moderate defoliation (10–50 percent of their leaf

Fig. 2. — (A) Ultimate-instar caterpillar of *Aellopos titan*; this green morph has a white lateral posterior diagonal stripe and light lateral diagonal white and magenta side stripes; it is the most common morph. (B) Ultimate-instar caterpillar of *A. titan*; this dark morph is dorsally lavender and ventrally black, with white lateral markings. It is the rare morph except during crowding, heavy shading, or total defoliation. The previous two instars of *A. titan* are extremely similar to these caterpillars. 20 June 1983, Santa Rosa National Park, Costa Rica.

surface area) or total leaf loss. In the latter case, the larvae present were wandering over the surface of the plant eating off petioles, leaf blade fragments, and buds. They were obviously a small remnant of much greater numbers of larvae on the tree. Finally, there were trees (25 percent) with 11 to several hundred larvae. For example, I counted, by removal sampling, 246 last-instar caterpillars from one *R. subcordata,* and there were at least another 200 on the tree (Fig. 3). At the time of the census, these densely populated trees still had 10–30 percent of their leaf surface remaining; however, within 5 days, when all larvae had been preyed upon or had left the tree to pupate, all of these leaves had been eaten. Such trees appeared to have had caterpillars that were slightly delayed in their development or initially to have had fewer caterpillars on them than those already stripped of their leaves had had. It was evident that complete defoliation (Fig. 3, 4) was a function of the number of caterpillars on a plant and the size of the plant. Part of the heterogeneity of defoliation was generated purely by this interaction.

The large ultimate- and penultimate-instar larvae (Fig. 2), were eaten by small to medium-sized birds, reduviid bugs, scorpions, and unidentified mammals. One mammal scat, of a size that could have been produced by a gray fox, small cat, or procyonid, contained 26 head capsules of penultimate and ultimate instar *A. titan* larvae. While such an enormous population of moth larvae would seem to be an easy substrate for intense parasitization, of 617 ultimate and penultimate instar larvae collected and reared, only seven caterpillars were parasitized by tachinids, and none contained parasitic Hymenoptera (Table 1).

The prepupal wandering stage of *A. titan* walks or drops off a plant and burrows into the litter to pupate. Of those which pupated in captivity, all living individuals emerged from the pupal

Fig. 3. — *Randia subcordata* adult tree defoliated by *Aellopos titan*; 3 days before this photograph was taken, this tree had at least 446 ultimate-instar *A. titan* caterpillars on it. The top of the parachute background is 3.8 m above the ground at each end. 23 June 1983, Santa Rosa National Park, Costa Rica.

Fig. 4 — *Randia karstenii* subadult treelet defoliated by *Aellopos titan*. 23 June 1983, Santa Rosa National Park, Costa Rica.

stage about 13–15 days after pupation (between 6 and 20 July). Pupal-stage duration was not influenced by wet or extremely dry conditions. The newly emerging adults simply left the site where they had developed; they were not observed at flowers that are standard nectar hosts for *Aellopos* (e.g., *Cedrela odorata* L., which were visited by hundreds of female moths at the time of oviposition in early June). Despite extensive and intensive nocturnal searches of *Randia* shrubs from mid-July to the end of August, only three *A. titan* larvae were located. There was no evidence of an attempted or realized second generation of the moth at this site or in other parts of the Santa Rosa forest.

The pupae in the litter were subject to moderate predation by vertebrates. Collared peccaries [*Tayassu tajacu* (L.)] and nine-banded armadillos (*Dasypus novemcinctus* L.) snuffled intensively through the litter below the *Randia* that had had large numbers of caterpillars, and I presume they were harvesting *A. titan* pupae. Spiny pocket mice [*Liomys salvini* (Thomas)] ate the pupae readily in the laboratory and foraged incessantly at night in the forest litter for seeds and insect pupae; on one occasion a mouse brought an *A. titan* pupa into a live trap and ate part of it there. However, living *A. titan* pupae could easily be found by sorting through litter until the time of adult eclosion in mid-July, and numerous newly eclosed adults were encountered on the foliage at that time. There is no doubt that despite the various sources of mortality mentioned above and later, a large number of adults eclosed in Bosque San Emilio and in other patches of deciduous forest in Santa Rosa.

Two weeks after the *A. titan* larvae had disappeared from the *Randia*, I walked a line transect through the Bosque San Emilio and estimated the intensity of defoliation of all *Randia* encountered (14 July 1983). Of 173 *R.*

Table 1. — Fate of 617 penultimate and ultimate instar *Aellopos titan* larvae collected from *Randia subcordata* and *R. karstenii* in Bosque San Emilio, Santa Rosa National Park, Costa Rica (1983).

| Date and Host | (n) | Percent Eclosed | Killed by Disease |  |  | Parasitized Larvae |
|---|---|---|---|---|---|---|
|  |  |  | As Larvae | As Pupae | Total |  |
| 18 June *R. s.* | (109) | 60 | 15 | 26 | 41 | 0 |
| 18 June *R. k.* | (117) | 60 | 17 | 21 | 38 | 1 |
| 19 June *R. s.* | (234) | 42 | 28 | 28 | 56 | 3 |
| 20 June *R. s.* | (79) | 82 | 4 | 14 | 18 | 3 |
| 23 June *R. s.* | (50) | 90 | 0 | 10 | 10 | 0 |
| 24 June *R. k.* | (28) | 93 | 0 | 7 | 7 | 0 |

*subcordata*, 41 percent were leafless (Fig. 3), 28 percent were moderately but conspicuously defoliated (often with one part of the crown more severely defoliated than another), and the remainder (31 percent) showed only traces of the feeding damage characteristic of *A. titan* larvae. Of 181 *R. karstenii* encountered, 63 percent were essentially leafless (Fig. 4), 30 percent were moderately defoliated, and the remainder appeared intact but had probably been fed on. Since *R. karstenii* leaves are very small and have a weak midrib, the larvae generally ate the entire leaf; small amounts of damage were therefore harder to recognize than they were on *R. cordata*. By the last half of August, all of the defoliated plants were putting out a new leaf crop and appeared approximately as they did during the first week of June. On 15 June 1983, a transect of forest along Quebrada Costa Rica (about 5 km SW of Bosque San Emilio and slightly drier) located 51 *R. karstenii*. All of these plants had lost all of their leaves to *A. titan*.

During the 1979–1982 growing seasons there was no defoliation of *Randia* by *A. titan* (or by any other insect). Frequent searches of numerous *Randia* plants during these 4 years yielded eight *Aellopos* larvae from Bosque San Emilio forest, six of which were parasitized by tachinids or Hymenoptera. The enormous number of adult female *A. titan* which appeared, as if by magic, in the Santa Rosa deciduous forest 25–28 May 1983 must have come from elsewhere, and when their offspring eclosed, they went elsewhere. Whether they arrived as a consequence of having concentrated in a large down-wind area in response to the odor of newly foliating *Randia*, or whether some more complex congregation event occurred, is beyond the scope of this essay.

My field notes from the 1978 rainy season suggest that there was a high density of *A. titan* on *Randia* in the Bosque San Emilio in late May and early June. While I was not collecting caterpillars in the field at that time, other biologists brought me 23 casually encountered *A. titan* larvae from "*Randia*" in this forest.

This account suggests several questions pertinent to this essay. Why did the newly eclosed adults not attempt a second generation at Santa Rosa by ovipositing on the foliated *Randia*? Why were predation and parasitization rates not high enough to eliminate the first generation or at least depress it to the levels of the 1979–1982 rainy seasons? Why was the final result of this "outbreak" a very heterogeneously defoliated array of *Randia* trees?

## No second generation

At the time of *A. titan* eclosion (early to mid-July), the undefoliated *Randia* had at least 5, perhaps 6, months of leafiness ahead of them. Since the egg-to-adult time for *A. titan* is about 35 days, there is ample time in the rainy season for at least three generations. Throughout the 1979–1982 rainy seasons, there were such generations at extremely low densities. In 1981, I recorded *A. titan* oviposition on *R. subcordata* as late in the rainy season as 10 January. In mid-August 1983, I encountered two last instar larva on *R. subcordata* and a single last instar larva on *R. karstenii*, but it was clear that no large pulse of eggs and larvae appeared on *Randia* foliage in July as it did in late May and early June.

Therefore it is clear that the newly eclosing *A. titan* females were confronted with a moderate number of leafy *Randia*, but either they rejected them as oviposition sites and went elsewhere or were programmed to leave the site irrespective of available food. Ironically, a leafy *Randia* that has escaped a defoliation event is probably an unsuitable oviposition site. If *Randia* are foliated because of leaf chemistry (unlikely; see below), then the female should not oviposit on leafy *Randia*. In contrast, until the second half of

August, defoliated individuals did not have enough leaves to support even a few caterpillars. They were leafless at the time of eclosion of the first generation. If, as I suspect, the foliated *Randia* is an indicator of high carnivory risk to eggs and caterpillars, then again, it is not a good oviposition site; the leafless *Randia* suggests a low risk site but offers no food. Selection should favor females that will ignore foliated *Randia* at the site of their birth and search in space or time for sites not subjected to recent defoliation.

It is appropriate to add here that I have observed *A. titan* females to oviposit on the new, partly expanded leaves of *R. subcordata* and *R. karstenii* during all months of the rainy season at Santa Rosa. Furthermore, I have reared their caterpillars on leaves of all ages in all months of the rainy season. While newly foliating *Randia* in late May and early June have more newly expanding leaves than at any other time, the plants also have some newly elongating branchlets at all times of the growing season. There are always some oviposition sites for *A. titan* during the rainy season in the Santa Rosa deciduous forests, even if they will only oviposit on very young foliage.

## Relatively low carnivory rates

While eggs and larvae of *A. titan* suffered conspicuous and intense predation, it was not sufficient to eliminate a highly evident array of caterpillars. As a *Randia* was becoming fully defoliated, for the last 2–8 days virtually no search was necessary to see tens of *A. titan* caterpillars on its ever more naked branches and petioles. However, these plants were not being subjected to hoards of insectivorous birds, mammals, or carnivorous insects. During several hours of observing *Randia* heavily infested with ultimate and penultimate instar caterpillars, it was customary to encounter 5–10 reduviid bugs, each killing one caterpillar; several caterpillars being stung or carried off by ants; one or two being carried off by small to medium-sized birds; and several apparently starving to death because they had fallen or wandered off their host plant. Some plants clearly had all of their caterpillars removed by carnivores, while others retained large numbers even after many had been removed; however, carnivore density was simply not high enough nor their searching thorough enough to depress the *A. titan* caterpillar density on all trees to a level even approximating the low level "normally" observed.

Either the Santa Rosa carnivore density was exceptionally low in 1983 or exceptionally large numbers of *A. titan* eggs were laid there in early 1983. I have no formal census data on carnivore density at Santa Rosa in 1979–1982, but certainly the 1983 density of birds and other predators did not seem to be any lower than were the 1979–1982 levels.

I should add, incidentally, that these levels are much lower than those readily visible in, for example, a Minnesota or Michigan woodlot in late May. However, I can state that there was no massive input of *A. titan* eggs and larvae in the 1979–1982 rainy seasons.[1]

The startlingly low numbers of parasitized *A. titan* larvae (Table 1) are consistent with records for other species of caterpillars at Santa Rosa that have suddenly increased greatly in density (unpublished field records). A hypothesis consistent with this low rate of parasitization is that the enormous number of larvae satiated the ovipositional capacity of the parasitoids present. It was striking that four of the seven parasitized larvae had different species of parasitoids in them and that none of the parasitoids were species that I had reared from *A. titan* in the past.

While I could not monitor disease levels in the field, the results of rearing

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[1] Note added in press: Likewise, in the 1984 and 1985 rainy seasons at Santa Rosa there was no massive input of *A. titan*.

penultimate and ultimate instar wild-caught caterpillars show clearly that disease was taking a severe toll of the caterpillars. The 617 caterpillars collected on 18–24 June (Table 1) were placed in individual plastic bags and were fed with foliage from plants lightly to moderately defoliated by *A. titan* (no plants were available with no *A. titan* damage). The bags were new or had been used (less than 1 percent) to house pupae of undiseased Saturniidae. Overall 39 percent of the caterpillars died of an unknown disease as larvae and as pupae of all ages. By way of contrast, *Aellopos* penultimate or ultimate instar larvae collected during 1979–1982 at Santa Rosa (three species on four host plant species, $n = 53$) invariably produced either adults or parasitoids, even though they were reared in exactly the same manner. The data in Table 1 suggest that the larger the collection of caterpillars, the fewer are killed by disease. However, the relationship actually lies with the age of the caterpillars at the time of collection. The 19 June sample contained the largest number of penultimate instars and the 23 and 24 June samples contained only ultimate instars with 1–3 days remaining before pupation. In the earliest samples, there were infected caterpillars that were fated to die in nature as larvae and that then died in my rearing bags. In the latest samples, those caterpillars that were fated to die in nature as caterpillars had already done so.

It is unlikely that the *A. titan* "outbreak" escaped annihilation because the predators and parasitoids were occupied elsewhere with some other species of prey. The overall caterpillar density in Bosque San Emilia in 1983 was conspicuously lower than in 1979–1982. Furthermore, 5 weeks, one *A. titan* generation, is insufficient time for a functional response by the predator and parasite array. A numerical response depends on both the distance over which the carnivores must move and the areal extent of the high density of prey. Little can be said about either in this tropical habitat, but it was clear that the high density of *A. titan* larvae covered hundreds of hectares. Also, this part of Costa Rica is not replete with large numbers of, for example, small insectivorous birds that could or would move to an "outbreak" of this sort.

In short, it appears that the local carnivores did not eliminate the *A. titan* outbreak because there were not enough of them to do so. I suspect that this was the case because (1) the outbreak occurred during the first weeks of the rainy season before whatever seasonal increase in carnivores that might occur had occurred, and (2) the habitat is not rich enough in prey to maintain a sufficiently high level of carnivores that they could consume a prey pulse with the properties of the *A. titan* caterpillars. Such an answer contains the implicit assumption that *A. titan* caterpillars are not suitable or available prey to a moderately large portion of the diverse carnivore array at Santa Rosa. The reasons range from physiological incompatibility to size and behavior. For example, the *Enicospilus* (Ichneumonidae) parasitoids that were heavily parasitizing large *Rothschildia lebeau* (Guer.-Meneville) (Saturniidae) larvae at the same time in the same forest, have never been encountered in over a thousand rearings of *Aellopos* and other Sphingidae caterpillars in Santa Rosa. The *Pseudomyrmex* and *Azteca* ants that so eagerly kill and carry off first and second instar *A. titan* larvae show no attack response to penultimate and ultimate instar *A. titan* larvae. Coatis [*Nasua nasua* (L.)] readily eat the larvae but do not readily climb the very thin and spiny branches of *Randia*. White-faced monkeys [*Cebus capucinus* (L.)] generally do not forage as low as 1–3 m above the ground in the forest interior during the rainy season and might well have never noticed the outbreak going on below them. The few species of North American migrant birds that visit Guanacaste during the northern winters had long since departed (see Janzen 1980).

## Heterogeneous defoliation

The array of predators in a tropical forest possesses sufficient patterned variation in its foraging to generate heterogeneous defoliation from an initial high level and thoroughly spread layer of eggs and caterpillars. One *Randia* may be close to and foraged extensively on by a colony of *Azteca* or *Camponotus* ants, and another only a few meters away may only be passed through by an occasional far-wandering *Pseudomyrmex* ant. A *Campylorhynchus* wren family may have only a single *Randia* in its foraging territory and may therefore thoroughly glean it of its caterpillars; another wren family may have 20 *Randia* in its territory and therefore only moderately glean several and ignore the remainder (F. Joyce, Division of Ecology and Systematics, Cornell University, personal communication). A reduviid bug that settles on a small *Randia* with 10 half-grown caterpillars may well kill all of them before they have done serious defoliation; the same bug on a neighboring tree with 30 caterpillars will at best only slow the time to total defoliation by a few days, since the surviving 20 caterpillars will be quite enough to eat all the leaves off the tree. Had only a few *A. titan* eggs been laid in the forest (as in 1979–1982), heterogeneity of predation would still have occurred, but the consequence would have been invisible against the background of the initial heterogeneity of oviposition. Had there been no carnivory in 1983, all the leaves would have been eaten off all the *Randia* trees, and there would have been major *A. titan* death by starvation. It can be argued that the failure of females to avoid previously laid eggs when ovipositing may well be due to the absence of selection for such behavior if it is usual for the number of surviving offspring to be unrelated to the number of offspring initially present on the plant. Her best chance is to distribute her eggs thinly over the *Randia* population, thereby maximizing the chance of placing some eggs on those *Randia* where there is low risk from predators.

The strong heterogeneity of defoliation could, at least in theory, also have been generated by heterogeneity in the suitability of the *Randia* foliage in terms of nutrients and secondary chemical defenses. Numerous natural history facts and suppositions argue against this possibility:

1. When second- to fifth-instar larvae were removed from *Randia* that they had defoliated and then were placed on *Randia* that had lost their initial caterpillars, they fed, developed, and pupated normally whether this was done in the field (under a protective net) or in plastic bags in the laboratory. In the laboratory, all larvae produced adults that were smaller than wild adults. However, they were equally dwarfed if they were fed leaves from their partly defoliated tree or leaves from trees quite free from damage (i.e., living in a plastic bag is suboptimal).

2. Defoliation was a function of tree size as well as of caterpillar numbers. A representative 2-m tall tree with 30 developing middle-sized larvae on it was defoliated by the time they left the tree to pupate; a 4-m tall tree with the same number of larvae suffered only minor damage, since it had many more leaves than did the smaller tree.

3. At least 40 different and foliated *Randia subcordata* trees were defoliated by harvesting their leaves to feed larvae in the laboratory. These larvae all developed normally with virtually no death except by disease, parasitoids, and laboratory accidents; their development time was not longer than that of their siblings left on *Randia* in the forest.

4. All foliated trees were fed on to some degree, and a careful search of many trees with no conspicuous damage revealed that one to five large and healthy caterpillars were feeding on them. When the foliage from these

trees was offered to second-instar larvae in the laboratory, these larvae fed readily and developed into normal adults.

It is tempting to wish that one could a priori know which trees were to be defoliated and therefore could obtain a leaf sample whose chemistry could be compared with those of leaves from trees not defoliated. However, this procedure was, and is, impossible when the moth has only one defoliating generation at a site in a season. Furthermore, all *Randia* individuals were fed on by at least one or more caterpillars; defoliation was a matter of degree. Finally, there is the problem of knowing what chemicals to search for in such a comparison. It might well turn out that the eventually defoliated trees would be found to differ chemically from those that were not defoliated. However, there would be no reason to believe that these particular chemical differences, rather than some other covarying plant traits, were responsible for the final levels of defoliation.

## HETEROGENEITY AMONG LIFE FORMS AND HABITATS

The risk of carnivory is important to caterpillars (e.g., Heinrich & Collins 1983; Holmes et al. 1979). This risk is not uniformly distributed among plant life forms (e.g., Thompson 1983; Royama 1970; Niemela et al. 1982) nor among the habitat types associated with different life forms. For example, a single large caterpillar in the crown of a large tree that projects above the vegetation should have a quite different probability of being located by a bird than if it were in the crown of a small sapling of the same species of tree projecting from young secondary succession. Likewise, a caterpillar in prey-rich, forest-edge herbaceous vegetation is more likely to be encountered by a *Polistes* wasp than if it were in the prey-poor canopy of a patch of evergreen forest. At Santa Rosa, the distribution of saturniid and sphingid caterpillars among their host plants provides an example.

At Santa Rosa, there are 30 breeding populations of Saturniidae (Janzen 1982) and at least 63 breeding populations of Sphingidae (Janzen 1984b). In an ongoing study, I have located at least one native host plant for 80 percent of the saturniids and 77 percent of the sphingids known or strongly suspected to breed at Santa Rosa (Tables 2 and 3). After examining only the host Latin binomials and caterpillar family names in Tables 2 and 3, it is evident that the huge caterpillars of sphingids and saturniids have little in common in their use of food plants (Janzen 1984b). Furthermore, at least half of the overlap in the two lists is a more apparent than a real similarity of food choice.

In keeping with current emphases on the causes of host specificity, several years ago a slightly reduced subset of the plants in Tables 2 and 3 was analyzed for phenolics and alkaloids (Janzen & Waterman 1983). The foliage of the saturniid hosts was found to contain significantly more phenolics and less water than did that of the sphingid hosts, while the sphingid hosts much more frequently contained alkaloids than did the saturniid hosts. These results are in strong agreement with two general impressions held by lepidopterists: (1) Most saturniids feed on tree foliage (traditionally viewed as rich in tannins), and (2) most sphingids feed on plants in families famous for toxic small molecules, resins, and copious latex flow. While not meaning to denigrate the reality of these patterns, there is obviously a quite different way to view the same set of host records.

It is evident that, as found in nature, the saturniid caterpillars are generally in the crowns of adult trees, while the sphingid caterpillars are found in plants ranging from small herbs to vines to saplings to crowns of large trees (Tables 2 and 3). The most

Table 2. — Larval hosts of Saturniidae in nature in Santa Rosa National Park, Costa Rica (as of December 1983).

| Larva | Host | Microhabitat |
|---|---|---|
| Arsenurinae | | |
| *Arsenura armida* (Cram.) | *Bambacopsis quinatum* (Jacq.) Dugand (Bombacaceae) | large tree crown |
| *Caio championi* (Drc.) | *Bambacopsis quinatum* (Jacq.) Dugand (Bombacaceae) | large tree crown |
| *Copiopteryx semiramis* (Cram.) | *Manilkara chicle* (Pittier) Gilly (Sapotaceae) | large tree crown |
| *Dysdaemonia bareas* (Cram.) | *Ceiba pentandra* (L.) Gaerth. (Bombacaceae)[a] | large tree crown |
| *Titaea tamerlan* (Maassen) | *Bombacopsis quinatum* (Jacq.) Dugand (Bombacaceae) | large tree crown |
| Ceratocampinae | | |
| *Adeloneivaia isara* (Dognin) | *Lysiloma divariciata* (Jacq.) Macbride (Leguminosae) | large tree crown |
| | *Lysiloma auritum* (Schl.) Benth. (Leguminosae) | large tree crown |
| *Citheronia bellavista* (Draudt) | *Phoradendron quadrangulare* (HBK) Krug & Urb. (Loranthaceae)[b] | parasite in crown of large tree |
| *Citheronia lobesis* (W. Rothschild) | *Cochlosperum vitifolium* (Willd.) Spreng. (Cochlospermaceae) | large saplings |
| | *Bursera simaruba* (L.) Sarg. (Burseraceae) | large tree crown |
| | *Spondias mombin* L. (Anacardiaceae) | large saplings |
| | *Psidium guajava* L. (Myrtaceae)[c] | shrubby treelet |
| | *Calycophyllum candidissimum* (Vahl.) DC. (Rubiaceae) | large tree crown |
| | *Phoradendron quadrangulare* (HBK.) Krug & Urb. (Loranthaceae) | parasite in crown of large tree |
| *Eacles imperialis* (Dry.) | *Cochlospermum vitifolium* (Willd.) Spreng. (Cochlospermaceae) | large saplings and large tree crown |
| | *Bursera tomentosa* (Jacq.) Triana & Planch. (Burseraceae) | large tree crown |
| | *Astronium graveolens* Jacq. (Anacardiaceae) | large tree crown |
| | *Cedrela odorata* L. (Meliaceae) | large tree crown |
| *Othorene purpurascens* (Schaus) | *Manilkara chicle* Pittier (Gilly) Sapotaceae | large tree crown |
| *Otharene verana* (Schaus) | *Quercus oleoides* Cham. & Schlecht. (Fagaceae) | large tree crown |
| *Ptiloscola dargei* Lemaire | *Acacia tenuifolia* (L.) Willd. (Leguminosae) | saplings and large vine crown |
| *Schausiella santarosensis* Lemaire | *Hymenaea courbaril* L. (Leguminosae) | large tree crown |
| *Syssphinx colla* (Dyar) | *Pithecellobium saman* (Jacq.) Benth. (Leguminosae) | large tree crown |
| *Syssphinx mexicana* (Bdv.) | *Acacia collinsii* Safford (Leguminosae) | sapling to adult treelet crown |
| | *Acacia cornigera* L. (Leguminosae) | sapling to adult treelet crown |

Table 2. — Continued

| Larva | Host | Microhabitat |
|---|---|---|
| *Syssphinx molina* (Cram.) | *Pithecellobium saman* (Jacq.) Benth. (Leguminosae) | large tree crown |
| | *Cassia grandis* L. (Leguminosae)[c] | large tree crown |
| | *Albizzia adinocephala* (Donn. Sm.) Britt. & Rose (Leguminosae) | large tree crown |
| *Syssphinx quadrilineata* (G. & R.) | *Pithecellobium saman* (Jacq.) Benth. (Leguminosae) | large tree crown |
| Hemileucinae | | |
| *Automeris io* (F.) | *Crescentia alata* HBK. (Bignoniaceae)[c] | large tree crown |
| | *Mimosa pigra* L. (Leguminosae) | shrub |
| | *Cassia biflora* L. (Leguminosae) | shrub |
| | *Rhynchosia reticulata* (Swartz) DC. (Leguminosae) | herbaceous vine |
| | *Gliricidia sepium* (Jacq.) Walp. (Leguminosae) | sapling |
| *Automeris rubrescens* (Wlk.) | *Inga vera* Willd. (Leguminosae) | sapling |
| | *Rourea glabra* HBK. (Connaraceae) | scandent shurb |
| | *Guazuma ulmifolia* Lam. (Sterculiaceae) | large tree crown |
| | *Cassia biflora* L. (Leguminosae) | shrub |
| | *Querus oleoides* Cham. & Schlecht. (Fagaceae) | sapling |
| | *Cordia alliodora* (R. & P.) Oken (Boraginaceae) | sapling |
| | *Lonchocarpus minimiflorus* Donn. Smith (Leguminosae) | sapling |
| | *Calycophyllum candidissimum* (Vahl.) DC. (Rubiaceae) | large tree crown |
| | DHJ 12175 (Bignoniaceae) | sapling vine |
| | *Zuelania guidonia* (SW.) Britt. & Millsp. (Flacourtiaceae) | large tree crown |
| | *Crescentia alata* HBK. (Bignoniaceae)[c] | large tree crown |
| | *Cassia grandis* L. (Leguminosae) | large tree crown |
| *Automeris zugana* Drc. | *Annona purpurea* Moc. & Sesse (Annonaceae) | large tree crown |
| | *Lonchocarpus costaricensis* Pittier (Leguminosae) | large tree crown |
| | *Querus oleoides* Cham. & Schlecht. (Fagaceae) | large tree crown |
| | *Cydista heterophylla* Seib. (Bignoniaceae) | large woody vine |
| | *Calycophyllum candidissimum* (Vahl.) DC. (Rubiaceae) | sapling to large tree crown |
| | *Hymenaea courbaril* L. (Leguminosae) | sapling |
| | *Solanum hazenii* Britt. (Solanaceae) | large herb |
| | *Lantana camara* L. (Verbenaceae)[c] | large herb/shrub |
| | *Lonchocarpus eriocarinalis* Micheli (Leguminosae) | large tree crown |
| | *Centrosema pubescens* Benth. (Leguminosae) | herb vine |

Table 2. — Continued

| Larva | Host | Microhabitat |
|---|---|---|
| | *Cassia hayesiana* (B. & R.) Standl. (Leguminosae) | shrub/treelet |
| | *Inga vera* Willd. (Leguminosae) | sapling |
| | *Serjania atroliniata* Sauv. & Wr. (Sapindaceae) | large vine |
| *Dirphia avia* (Stoll) | *Hymenaea courbaril* L. (Leguminosae) | large tree crown |
| | *Cedrela odorata* L. (Meliaceae) | large tree crown |
| *Hylesia dalina* Schaus | *Casearia arguta* HBK. (Flacourtiaceae) | treelet |
| | *Malvaviscus arboreus* Cav. (Malvaceae) | shrub |
| *Hylesia lineata* Drc. | *Tabebuia rosea* (Vertol.) DC. (Bignoniceae) | sapling |
| | *Bombacopsis quinatum* (Jacq.) Dugand (Bombacaceae) | large tree crown |
| | *Cordia alliodora* (R. & P.) Oken (Boraginaceae) | treelet |
| | *Hirtella racemosa* Lam. (Chrysobalanaceae) | treelet |
| | *Muntingia calabura* (Swartz) DC. (Elaeocarpaceae) | treelet |
| | *Casearia arguta* HBK. (Flacourtiaceae) | treelet |
| | *Casearia sylvestris* SW. (Flacourtiaceae) | treelet |
| | *Casearia corymbosa* HBK. (Flacourtiaceae) | treelet |
| | *Zuelania guidonia* (SW.) Britt. & Millsp. (Flacourtiaceae) | large tree crown |
| | *Acacia tenuifolia* (L.) Willd. (Leguminosae) | large vine crown |
| | *Cassia biflora* L. (Leguminosae) | shrub |
| | *Diphysa robinioides* Benth. (Leguminosae) | sapling |
| | *Enterolobium cyclocarpum* (Jacq.) Griseb. (Leguminosae) | large tree crown |
| | *Hymenaea courbaril* L. (Leguminosae) | sapling |
| | *Inga vera* Willd. (Leguminosae) | treelet |
| | *Lonchocarpus minimiflorus* Donn. Smith. (Leguminosae) | treelet |
| | *Lonchocarpus costaricensis* Pittier (Leguminosae) | sapling |
| | *Lysiloma auritum* (Schl.) Benth. (Leguminosae) | large tree crown |
| | *Machaerium kegelii* (Meisner) (Leguminosae) | sapling large vine |
| | *Mimosa pigra* L. (Leguminosae) | shrub |
| | *Myrospermum frutescens* Jacq. (Leguminosae) | treelet |
| | *Pithecellobium lanceolatum* (H. & B.) Benth. (Leguminosae) | treelet |
| | *Hyptis pectinata* Poit. (Labiatae) | large herb |
| | *Malvaviscus arboreus* Cav. (Malvaceae) | shrub |
| | *Banisteriopsis muricata* (Cav.) Cuatr. (Malpighiaceae) | low vine |

Table 2. — Continued

| Larva | Host | Microhabitat |
|---|---|---|
| | *Byrsonima crassifolia* (L.) HBK. (Malpighiaceae) | treelet |
| | *Stigmaphyllon ellipticum* (HBK.) Adr. Juss. (Malpighiaceae) | low vine |
| | *Psidium guineense* SW. (Myrtaceae) | shrub |
| | *Ouratea lucens* (HBK.) Engler (Ochnaceae) | shrub |
| | *Gouania polygama* (Jacq.) Urban (Rhamnaceae) | low vine |
| | *Calycophyllum candidissiumum* (Vahl.) DC. (Rubiaceae) | sapling |
| | *Chomelia spinosa* Jacq. D. (Rubiaceae) | treelet |
| | *Guettarda macrosperma* D. Sm. (Rubiaceae) | treelet |
| | *Xanthoxylum setulosum* P. Wilson (Rutaceae) | sapling |
| | *Allophyllus occidentalis* (SW.) Radlk. (Sapindaceae) | treelet |
| | *Cupania guatemalensis* (Turcz.) Radlk. (Sapindaceae) | treelet |
| | *Paullinia cururu* L. (Sapindaceae) | low vine |
| | *Serjania schiedeana* Schlecht. (Sapindaceae) | low vine |
| | *Urvillea ulmacea* HBK. (Sapindaceae) | low vine |
| | *Byttneria aculeata* Jacq. (Sterculiaceae) | shrub |
| | *Byttneria catalpaefolia* Jacq. (Sterculiaceae) | low vine |
| | *Guazuma ulmifolia* Lam. (Sterculiaceae) | medium tree |
| | *Luehea speciosa* Willd. (Tilliaceae) | sapling |
| | *Lantana camara* L. (Verbenaceae) [c] | shrub |
| | *Erythroxylum havanense* Jacq. (Erythroxylaceade) | shrub |
| | *Calliandra emarginata* Benth. (Leguminosae) | shrub |
| *Periphoba arcaei* (Drc.) | *Eugenia salamensis* Donn. Sm. (Myrtaceae) | medium tree crown |
| | *Cassia biflora* L. (Leguminosae) | shrub |
| | *Guazuma ulmifolia* Lam. (Sterculiaceae) | large tree crown |
| | *Lysiloma auritum* (Schl.) Benth. (Leguminosae) | large tree crown |
| | *Spondias mombin* L. (Anacardiaceae) | large tree crown |
| | *Rourea glabra* HBK. (Connaraceae) | scandent shrub |
| | *Annona purpurea* Moc. & Sesse (Annonaceae) | treelet crown |
| | *Calycophyllum candidissimum* (Vahl.) DC. (Rubiaceae) | large tree crown |
| | *Bombacopsis quinatum* (Jacq.) Dugand (Bombacaceae) | large tree crown |

Table 2. — Continued

| Larva | Host | Microhabitat |
|---|---|---|
| | *Cassia alata* L. (Leguminosae)[c] | large tree crown |
| | *Inga vera* Willd. (Leguminosae) | medium tree crown |
| | *Ardisia revoluta* HBK. (Myrsinaceae) | treelet |
| | *Astronium graveolens* Jacq. (Anacardiaceae) | sapling |
| | *Hymenaea courbaril* L. (Leguminosae) | sapling |
| | *Quercus oleoides* Schlecht. & Cham. (Fagaceae) | large tree crown |
| | *Miconia argentea* (Swartz) DC. (Melastomataceae) | sapling |
| Saturniinae | | |
| *Copaxa moinieri* Lemaire | *Ocotea veraguensis* (Meisn.) Vlez (Lauraceae) | saplings and lower branches of treelet |
| *Rothschildia erycina* (Shaw) | *Exostema mexicanum* (Jacq.) Roem. & Schult. | large tree crown |
| | *Coutarea hexandra* (Jacq.) Schum. (Rubiaceae) | treelet crown |
| *Rothschildia lebeau* (Guer.-Meneville) | *Exostema mexicanum* Jacq. Roem. & Schult. (Rubiaceae) | large tree crown |
| | *Spondias mombin* L. (Anacardiaceae) | large tree crown |
| | *Spondias purpurea* L. (Anacardiaceae) | treelet |
| | *Casearia corymbosa* HBK. (Flacourtiaceae) | treelet |
| | *Zuelania guidonia* (Sw.) Britt. & Rose (Flacourtiaceae) | large tree crown |
| | *Xanthaxylum setulosum* P. Wilson (Rutaceae) | large tree crown |

[a] Not yet found in nature but accepts readily and dies on other Santa Rosa Bombacaceae.

[b] Not yet found in nature but accepts readily and has the appropriate color and behavior to use this host.

[c] Plant introduced to Santa Rosa within past several hundred years.

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Table 3. — Larval hosts of Sphingidae in nature in Santa Rosa National Park, Cost Rica (as of December 1983).

| Larva | Host | Microhabitat |
|---|---|---|
| *Aellopos clavipes* (R. & J.) | *Randia karstenii* Polak (Rubiaceae) | sapling to treelet |
| *Aellopos fadus* (Cram.) | *Genipa americana* L. (Rubiaceae) | sapling to large tree |
| | *Alibertia edulis* A. Rich. (Rubiaceae) | shrub |
| *Aellopos titan* (Cram.) | *Randia karstenii* Polak (Rubiaceae) | sapling to treelet |
| | *Randia subcordata* (Stand.) Standley (Rubiaceae) | sapling to treelet |
| *Agrius cingulatus* (F.) | *Merremia umbellata* (L.) Hall (Convolvulaceae) | herb vine |

Table 3. — Continued

| Larva | Host | Microhabitat |
|---|---|---|
|  | DHJ 12071 (Convolvulaceae) | herb vine |
| *Aleuron carinata* Wlk. | *Doliocarpus dentatus* (Aubl.) Stand. (Dilleniaceae) | low perennial vine |
| *Aleuron iphis* Wlk. | *Tetracera volubilis* L. (Dilleniaceae) | low perennial vine |
| *Amplypterus gannascus* (Stoll) | *Ocotea veraguensis* (Meisn.) Vlez (Lauraceae) | sapling to treelet |
| *Amplypterus ypsilon* R. & J. | *Ocotea veraguensis* (Meisn.) Vlez (Lauraceae) | sapling to treelet |
| *Callionima falcifera* (Gehlen) | *Stemmadenia obovata* (Hook & Arn.) K. Schum. (Apocynaceae) | sapling to treelet |
| *Cautethia spuria* (Bdv.) | *Exostema mexicanum* A. Gray (Rubiaceae) | sapling to large tree |
|  | *Coutarea hexandra* (Jacq.) Schum. (Rubiaceae) | treelet |
| *Cautethia yucatana* B. P. Clark | *Exostema mexicanum* A. Gray (Rubiaceae) | treelet |
| *Cocytius duponchel* (Poey) | *Annona purpurea* Moc. & Sesse (Annonaceae) | sapling to treelet |
|  | *Annona reticulata* L. (Annonaceae) | sapling to treelet |
| *Enyo ocypete* (L.) | *Tetracera volubilis* L. (Dilleniaceae) | low perennial vine |
|  | *Cissus rhombifolia* Vahl. (Vitaceae) | herb vine |
| *Erinnyis ello* (L.) | *Sebastiana confusa* Lundell (Euphorbiaceae) | sapling to treelet |
|  | *Sapium thelocarpum* Schm. & Pitt. (Euphorbiaceae) | sapling |
|  | *Manilkara chicle* (Pittier) Gilly (Sapotaceae) | large tree |
| *Erinnyis lasauxii* (Bdv.) | *Sarcostemma glauca* HBK. (Asclepiadaceae) | low vine |
| *Erinnyis oenotrus* (Cram.) | *Fosteronia spicata* (Jacq.) G. Mey (Apocynaceae) | low perennial vine |
| *Eumorpha anchemola* (Gram.) | *Cissus rhombifolia* Vahl. (Vitaceae) | low perennial vine |
|  | *Cissus sicyoides* L. (Vitaceae) | low perennial vine |
| *Eumorpha satellitia* (L.) | *Cissus rhombifolia* Vahl. (Vitaceae) | low perennial vine |
|  | *Cissus sicyoides* L. (Vitaceae) | low perennial vine |
| *Eupyrrhoglossum sagra* (Poey) | *Chomelia spinosa* Jacq. (Rubiaceae) | sapling to treelet |
|  | *Guettarda macrosperma* D. Sm. (Rubiaceae) | sappling to treelet |
| *Isognathus rimosus* (Grt.) | *Plumeria rubra* L. (Apocynaceae) | large tree |
| *Manduca barnesi* (Clark) | *Godmania aesculifolia* (HBK.) Standl. (Bignoniaceae) | sapling |
| *Manduca corallina* (Drc.) | *Cordia alliodora* (R. & P.) Oken (Boraginaceae) | sapling to large tree |
| *Manduca dilucida* (Hy. Edw.) | *Sapranthus palanga* Fries (Annonaceae) | sapling to treelet |
|  | *Annona reticulata* L. (Annonaceae) | sapling to treelet |
| *Manduca florestan* (Cram.) | *Pithecoctinium crucigerum* (L.) A. Gentry (Bignoniaceae) | low perennial vine |
|  | *Cydista heterophylla* Seib. (Bignoniaceae) | low perennial vine |
|  | *Tabebuia ochracea* (Cham.) Standl. (Bignoniaceae) | sapling |
|  | *Callichlamys latifolia* (L. Rich) K. Schum. (Bignoniaceae) | low perennial vine |
|  | *Arrabidaea chica* (H. & B.) Verl. (Bignoniaceae) | low perennial vine |
|  | *Cornutia grandifolia* (Schlecht. & Cham.) Schau. (Verbenaceae) | shrub |
|  | *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandw. | low perennial vine |

Table 3. — Continued

| Larva | Host | Microhabitat |
|---|---|---|
| | *Plenontoma voriabilis* (Jacq.) Miers (Bignoniaceae) | low perennial vine |
| | *Stachytarpheta frantzii* Polak (Verbenaceae) | shrub |
| *Manduca lefeburei* (Guer.) | *Casearia sylvestris* SW. (Flacourtiaceae) | sapling to treelet |
| | *Casearia corymbosa* HBK. (Flacourtiaceae) | sapling to treelet |
| *Monduca muscosa* (R. & J.) | *Verbesina gigantea* Jacq. (Compositae) | giant herb |
| | *Lantona camara* L. (Verbenaceae) | shrub |
| | *Lasianthaea fruticosa* (L.) K. Becker (Compositae) | shrub |
| | *Baltimora recta* L. (Compositae) | herb |
| | *Melanthera ospera* (Jacq.) Small (Compositae) | herb |
| | *Wedelia calycina* L. C. Rich (Compositae) | herb |
| *Manduca occulta* (R. & J.) | *Solanum ochraceo-ferrugineum* (Dun.) Fern (Solanaceae) | herb |
| | *Solanum hazenii* Britt. (Solananceae) | herb |
| | *Solanum accrescens* Standl. & Mort. (Solanaceae) | herb |
| | *Cestrum* DHJ 12029 (Solanaceae) | shrub |
| *Manduca rustica* (F.) | *Lantana camara* L. (Verbenaceae)[a] | shrub |
| | *Stachytarpheta frantzii* Polak (Verbenaceae) | shrub |
| | *Cordia panamensis* Riley (Boraginaceae) | sapling |
| | *Pithecoctenium crucigerum* (L.) A. Gentry (Bignoniaceae) | low perennial vine |
| | *Amphilophium paniculatum* (L.) HBK. (Bignoniaceae) | low perennial vine |
| | *Merremia umbellata* (L.) Hall (Convolvulaceae) | herb vine |
| | DHJ 12071 (Convolvulaceae) | herb vine |
| | *Hyptis verticillata* Jacq. (Labiatae) | herb |
| *Manduca sexta* (L.) | *Capsicum annum* L. (Solanaceae) | herb |
| | *Lycopersicon esculentum* MIll. (Solanaceae)[a] | herb |
| *Neococytius cluentius* (Cram.) | *Piper marginatum* Jacq. (Piperaceae) | shrub |
| *Nyceryx coffeae* (Wlk.) | *Calycophyllum candidissimum* (Vahl.) DC. (Rubiaceae) | sapling to large tree |
| *Pachygonia drucei* R. & J. | *Doliocarpus dentatus* (Aubl.) Stand. (Dilleniaceae) | low perennial vine |
| *Pachylia ficus* (L.) | *Ficus insipida* Willd. (Moraceae) | sapling to large tree |
| | *Ficus continifolia* HBK. (Moraceae) | sapling to large tree |
| | *Ficus obtusifolia* HBK. (Moraceae) | sapling to large tree |
| | *Ficus ovalis* (Liebm.) Miq. (Moraceae) | sapling to large tree |
| | *Brosimum alicastrum* Swartz. (Moraceae) | sapling |

Table 3. — Continued

| Larva | Host | Microhabitat |
|---|---|---|
| | *Chlorophora tinctoria* (L.) Gaud. (Moraceae) | sapling to large tree |
| | *Castilla elastica* Cerv. (Moraceae) | sapling |
| *Pachylia syces* (Hbn.) | *Ficus ovalis* (Liebm.) Miq. (Moraceae) | large tree |
| *Pachylioides resumens* (Wlk.) | *Forsteronia spicata* (Jacq.) Mull (Apocynaceae) | low perennial vine |
| *Perigonia lusca* (F.) | *Calcophyllum candidissimum* (Vahl.) DC. (Rubiaceae) | sapling to large tree |
| | *Guettarda macrosperma* D. Sm. (Rubiaceae) | sapling to treelet |
| *Protambulyx strigilis* (L.) | *Astronium graveolens* Jacq. (Anacardiaceae) | sapling to large tree |
| | *Spondias mombin* L. (Anacardiaceae) | sapling to large tree |
| *Pseudosphinx tetrio* (L.) | *Plumeria rubra* L. (Apocynaceae) | large tree |
| *Sphinx merops* Bdv. | *Lantana camara* L. (Verbenaceae)[a] | shrub |
| | *Hyptis pectinata* Poit. (Labiatae) | herb |
| *Unzela pronoe* (Drc.) | *Tetracera volubilis* L. (Dilleniaceae) | low perennial vine |
| *Xylophanes anubus* (Cram.) | *Psychotria nervosa* Sw. (Rubiaceae) | shrub |
| | *Psychotria horizontalis* Sw. (Rubiaceae) | shrub/herb |
| *Xylophanes ceratomioides* (G. & R.) | *Hamelia patens* Jacq. (Rubiaceae) | shrub |
| *Xylophanes chiron* Dry. | *Psychotria pubescens* Sw. (Rubiaceae) | shrub |
| | *Psychotria horizontalis* Sw. (Rubiaceae) | shrub |
| | *Faramea occidentalis* (L.) A. Rich. (Rubiaceae) | sapling |
| *Xylophanes juanita* R. | *Psychotria pubescens* Sw. (Rubiaceae) | shrub |
| | *Psychotria horizontalis* Sw. (Rubiaceae) | shrub/herb |
| | *Psychotria nervosa* Sw. (Rubiaceae) | shrub |
| *Xylophanes maculator* (Bdv.) | Psychotria horizontalis Sw. (Rubiaceae) | shrub/herb |
| *Xylophanes pluto* (F.) | *Hamelia patens* Jacq. (Rubiaceae) | shrub |
| *Xylophanes porcus* (Hbn.) | *Hamelia patens* Jacq. (Rubiaceae) | shrub |
| *Xylophanes turbata* (Hy. Edw.) | *Hamelia patens* Jacq. (Rubiaceae) | shrub to treelet |
| | *Psychotria microdon* (DC.) Urban (Rubiaceae) | shrub/herb |
| *Xylophanes tyndarus* (Bdv.) | *Faramea occidentalis* (L.) A. Rich. (Rubiaceae) | treelet |

[a] Host plant introduced to Santa Rosa National Park.

revealing addendum to this pattern is that if those same saturniid caterpillars are placed on small saplings inside screen nets, they develop into quite normal adults. This is true whether they are transferred as first-instar or any later-instar caterpillars. I have done this with *Rothschildia lebeau* on *Spondias mombin* L. and *Xanthoxylum setulosum* P. Wilson; *R. erycina* (Shaw) on *Exostema mexicanum* A. Gray and *Coutarea hexandra* (Jacq.) Schum.; *Eacles imperialis* (Dry.) on *Cochlospermum vitifolium* (Willd.) Spreng.; *Citheronia lobesis* W. Rothschild on *Calycophyllum candidissimum* (Vahl.) DC., *Spondias mombin*, and *Cochlosperum vitifolium; Arsenura armida* (Cram.), *Caio championi* (Drc.), and *Titaea tamerlan* (Maassen) on *Bombacopsis quinatum* (Jacq.) Dugand; *Othorene purpurascens* (Schaus) on *Manilkara chicle* (Pittier) Gilly; *Othorene verana* (Schaus) on *Quercus oleoides; Syssphinx molina* (Cram.) on *Pithecellobium saman* (Jacq.) Benth., *Cassia grandis* L., and *Albizzia adinocephala* (Donn. Sm.) Britt. & Rose; *Syssphinx colla* (Dyar) on *Pithecellobium saman; Adeloneivaia isara* (Dognin) on *Lysiloma divaricata* (Jacq.) Macbride and *L. auritum* (Schl.) Benth.; and *Dirphia avia* (Stoll) and *Schausiella santarosensis* Lemaire on *Hymenaea courbaril*. The net protects the caterpillars from carnivores but does not, I assume, seriously modify the microclimate of the plant's physiology.

The opposite experiment, putting these species of saturniid larvae on a host plant sapling in nature without a protective net, results in rapid removal of the caterpillars by ants, wasps, birds, scorpions, mammals, and spiders. The few survivors are very often parasitized. I am in the process of conducting large-scale experiments which will yield an understanding of the variation and how it compares with the mean and variance of the same experiments in adult host plant crowns. However, a few preliminary results are instructive.

On 18 July 1983, I placed 340 first-instar, newly hatched *Rothschildia lebeau* caterpillars on a 4-m tall bushy *Spondias mombin* sapling growing in a tangle of secondary succession. The lower trunk was ringed with Tanglefoot, and the surrounding vegetation was trimmed so that the host plant did not contact any other plant. By 8 August, 21 days later, only 13 caterpillars remained, all late penultimate instar. On 15 August, 3–5 days before they were due to wander off the plant to pupate, I removed the 12 remaining survivors, all of which spun cocoons. Of these caterpillars, 5 contained a large ichneumonid wasp larva *(Enicospilus)*, 3 contained larvae of tachinid flies, 3 died of disease inside their cocoons before they could pupate, and 1 produced a healthy pupa.

On 30 June, I placed 120 third- and early fourth-instar larvae of *Syssphinx molina* on 60 sapling *Pithecellobium saman* growing in roadside secondary succession within 100 m of adult *P. saman*. Shortly before these larvae (Fig. 5A) were due to leave the plant to pupate in the litter and only 11 days after they had been placed out, I collected the 14 survivors. Three of these contained larvae of a species of *Thyreodon*, an ichneumonid wasp apparently specific to this caterpillar and its close relatives, and six produced healthy pupae; the remainder died of disease. As yet I have no extensive data on the survivorship of *Rothschildia lebeau* or *Syssphinx molina* caterpillars in the crowns of their large tree host plants, but numerous anecdotal observations suggest that it will be greater than the low levels of survival mentioned above.

There is a very conspicuous exception to the generality that saturniids are concentrated in the crowns of adult trees. Hemileucine saturniids, the io moth to extratropical New World readers, are found both on juveniles of their hosts and on species of plants that are normally small as adults and are therefore imbedded in low secondary succession (these caterpillars are found as well in the crowns of large trees; see Table 2). Hemileucine caterpillars (Fig. 5B, C) are the most severe urticators of

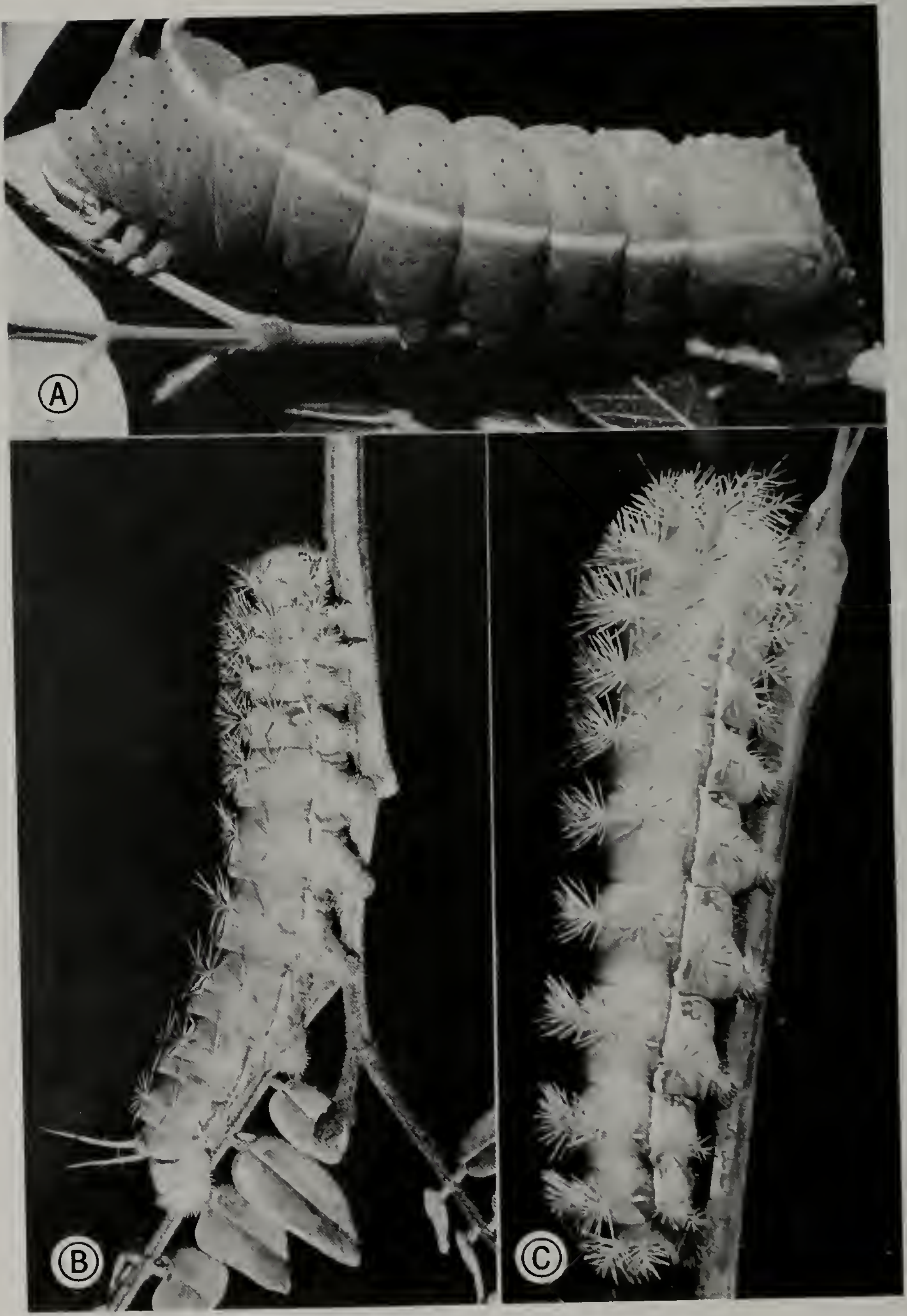

Fig. 5. — (A) Ultimate-instar larva of *Syssphinx molian*; this green morph has a greenish-white lateral stripe, yellow thoracic horns (scoli), and posterior dorsal gold toothlike spines. (B) Ultimate-instar urticating larva of *Periphoba arcaei*; this green caterpillar has a pale whitish-green lateral line with a lavender line just above it. (C) Ultimate-instar urticating larva of *Automeris io*; this green caterpillar has a white lateral line with a dark red lateral line just above it and lower lateral dark red patches with white dots. July-August 1983, Santa Rosa National Park, Costa Rica.

the saturniid world. As such they are largely invulnerable to a major subset of the vertebrate carnivores that probably find it more profitable to search for food in secondary succession than in the huge monospecific expanses of leaves in the forest canopy.

It is too early in this investigation to be able to offer a clean hypothesis about what allows sphingid caterpillars to feed on such a diversity of plant life forms (Table 3), especially on the small ones. However, some possibilities come to mind (cf. Janzen 1984b).

1. Sphingid adults live for weeks to months (as compared with 3–10 days for saturniid females) and therefore have more time to seek out widely scattered small individual hosts on which to lay only one or very few eggs at a time; with only a few nights to search for a host, a saturniid female may find it more profitable to search for a few large crowns and lay many eggs on each than to have to locate many saplings.

2. By being initially widely scattered, sphingid caterpillars avoid density-dependent effects, such as are likely to occur when, for example, a *Polistes* wasp finds one of many saturniid caterpillars on a plant and repeatedly returns to harvest them.

3. Because they are extremely host-specific, sphingid caterpillars are on average more cryptic than are saturniid caterpillars and therefore have a greater chance of surviving the visually oriented component of the more intense carnivory that, I suspect, occurs in the low vegetation of secondary succession.

4. Sphingid caterpillars grow more rapidly to a given size than do saturniids of the same body weight; they are therefore exposed to agents of larval mortality for a shorter period than are saturniid caterpillars.

5. Sphingid caterpillars may have chemical or physical defenses against invertebrate carnivores, defenses that saturniids lack. I have seen the same *Polistes* that aggressively harvests young *Caio championi* caterpillars from sapling *Bombacopsis* land on *Manduca sexta* (L.) caterpillars and simply walk on in search of food, apparently treating the caterpillars as though they were part of the plant.

Three species of "primitive" sphingids (Smerinthinae) at Santa Rosa offer instructive exceptions to the generality that sphingids and saturniids have different hosts at Santa Rosa. *Protambulyx strigilis* (L.) caterpillars are commonplace on *Spondias mombin* and *Astronium graveolens* Jacq., ranging from 1.5-m saplings to the crowns of 20-m, full-grown trees; they are found on all sizes of their hosts from forest understory to tree falls to large expanses of recent secondary succession along roads and in old fields. They are heavily parasitized by tachinids on all of these plant life forms and in all habitats. In forests, and on forest edges, *Rothschildia lebeau* (Saturniidae) caterpillars are found only in the crowns of medium-sized to large *Spondias mombin*; it is extremely difficult to imagine what besides predator pressure could have been responsible for the evolution or ecology of this restriction to adult *S. mombin*. However, since female *R. lebeau* do occasionally oviposit on sapling *S. mombin*, and I have on seven occasions found well-developed *R. lebeau* larvae on *S. mombin* saplings in secondary succession, it may be that there is little evolution involved. Rather, the *R. lebeau* females may be ovipositing throughout the *S. mombin* population, but carnivores may be eliminating those on the saplings. If this is the case, were *S. mombin* the only *R. lebeau* host plant in the park and were *S. mombin* a small treelet only found in early secondary succession, *R. lebeau* might well be absent from the park. It is also evident that *P. strigilis* is substantially more cryptic than is *R. lebeau* when on *S. mombin*.

*Amplyterus gannascus* (Stoll) and *A. ypsilon* R. & J., the other two smerinthine sphingids at Santa Rosa, feed exclusively on *Ocotea veraguensis*

(Meisn.) Vlez. *O. veraguensis* is a shrubby subcanopy treelet found throughout the understory of several forest types at Santa Rosa. It is the only lauraceous plant in the habitat. *A. gannascus* and *A. ypsilon* are encountered feeding on the foliage of *O. veraguensis* at all heights, from 1-m saplings to the tops of the crowns of 8-m tall large adult plants. The saturniid *Copaxa moinieri* Lemaire has *O. veraguensis* as its sole host at Santa Rosa. In contrast to other saturniids, *C. moinieri* is conspicuous in feeding entirely on the saplings and lower branches of its host and is virtualy never found more than 3 m above the ground. *O. veraguensis* may range from forest edge to heavily shaded forest understory, but the vast majority are in the forest understory. However, if the caterpillars are placed on foliage in crowns of adult *O. veraguensis* under protective nets or on similar foliage in plastic bags in the laboratory, they develop quite normally. Here again, the sphingid feeds throughout the life forms of its host plant, while the saturniid is restricted to a particular subset of its host population. While as yet untested, one selective pressure for this behavior is easy to postulate. Since the host is a forest understory plant, feeding solely on the foliage within about 3 m of the ground places caterpillars in a zone quite free of foraging by white-faced monkeys. White-faced monkeys are eager to eat large caterpillars, and in the last instars, the caterpillars of *C. moinieri* are quite easy to find because of the characteristic damage that they do when feeding. This is so when there is a defoliation event, at which time the leafless shrubs are cleaned of caterpillars by the human collector, and presumably would be as well by insectivorous monkeys if they foraged close to the ground.

There are at least six other species of *Copaxa* in Costa Rica. A summary of *Copaxa* host records (Janzen unpublished manuscript) suggests that they are specialists on Lauraceae and may be able eat the foliage of any species of *Ocotea*, *Nectandra*, or *Persea*. Why then don't they occur at Santa Rosa, where *O. veraguensis* is common? At least three species of *Copaxa* occur only 10–13 km to the east in a more evergreen forest that is continuous with the Santa Rosa forest. Could it be that these other species of *Copaxa* feed higher in the foliage of their host plant and therefore don't survive at Santa Rosa because this zone is lethal on *O. veraguensis* in the dry forest of lower stature, as found at Santa Rosa?

In short, when a sphingid hops to a new host plant, it gets more than the plant's chemistry. The plant's nutrient value may be high and its defenses may be easily bypassed by existing chemical pathways, but if a green caterpillar has to sit on a brown leaf all day, its fitness on that plant may well be zero. Likewise, if a species of saturniid caterpillar is essentially immune to most vertebrate carnivores because it has severely urticating spines, it has a major trait that predisposes it to the evolution of the biochemical ability to feed on a variety of host species. This appears to be the case with the hemileucine saturniids. They, severe urticators, are found on many kinds of leafy backgrounds, as indicated by their long host lists.

On the other hand, I do not wish to denigrate the importance of plant chemistry in all of this. If a caterpillar lineage comes up with a high quality general-purpose detoxifying system, as the ancestral species to the hemileucines must have done, then the mutant that subsequently invented urticating hairs had the companion trait necessary to allow the explosive radiation that produced and maintained the most species-rich and widespread of the four New World saturniid subfamilies. Over half the New World saturnids are hemileucines; the most species-rich genus, *Hylesia*, with over 200 species (C. Lemaire personal communication), has not only severely urticating caterpillars (see Janzen 1984a for a review), but aggregating caterpillars as well.

## CAN A CATERPILLAR GET A FREE RIDE?

A major aspect of the evolutionary accumulation of a plant species' herbivore load is the intensity of fitness depression of the plant by an evolutionarily incoming caterpillar. Put most simply, the more severe is the caterpillar's impact, the more likely is the newcomer to depress the density or local distribution of the plant to a level at which it will not support the caterpillar population or will select for a defense trait that will evict a portion of the herbivore load, or both. In short, one expects that the smaller the bite the herbivore takes, the more likely it is to be able to persist on a new host plant. But bites are measured not in grams of seeds or area of leaves, but in units of population change or fitness depression.

There is, however, one rarely discussed way in which a herbivore can take large bites without depressing the fitness of the host plant. If the herbivore feeds on a subset of the host population that is fated to die prior to reproduction irrespective of the herbivore's impact, it will have no fitness-depressive effect whatsoever. Additionally, if it feeds on a plant that will live to reproduce, then the fitness-depressing effect of its herbivory should be directly proportional to the fitness of that plant relative to its conspecifics. In other words, the worst way to move evolutionarily among host species or increase your host list is to take big bites out of the individuals of the population with the highest potential fitness. At the opposite extreme are the herbivores that feed on plants that are clearly genetically dead though physiologically living – the green aborted leaf or fruit on the forest floor, the branch newly broken out of the tree crown, the seed defecated on the floor of a dry bat cave, the annual herb that has matured and shed its seeds, and so on. A detritivore is defined as an organism that feeds on a dead plant (or animal), and from the viewpoint of evolutionary ecology, *dead* is defined as having zero potential fitness. While no living wild plant has zero probability of surviving to first reproduction, it is certain that the probability of attaining any given fitness value is neither distributed evenly among the members of the population nor at random with respect to a multitude of environmental variables. The questions become whether sufficient cues exist by which herbivory can be evolutionarily or ecologically directed so that its impact is reduced, and whether individual selection can generate the necessary traits. To ask the question in a different way, are there caterpillars with little or no impact on their host populations simply because they feed (for whatever reason) on that subset of the plant population that has severely reduced potential fitness?

Such a set of questions calls attention to a major difference between plants and animals as hosts or prey. Since animals move around, it is harder to identify individuals, cohorts, or arrays that have a high likelihood of not attaining full adult status than is the case with plants. Despite the fact that we all know about this difference, ecologists have not developed either a terminology or conceptual base with which to discuss easily its potential significance to competition, herbivory, edaphic responses, etc.

Before examining some examples at Santa Rosa, a hypothetical example is in order. First, consider the case of a monophagous caterpillar species that is distributed over its host plants in a manner unrelated to the probability of any particular plant's attaining its potential fitness. Assume the caterpillar to be on 20 percent of the host individuals and that each caterpillar set (on each plant) eats half the leaves off its plant before pupating. The 10 percent of the plant population with a moderate chance of becoming adult (e.g., individuals growing in tree falls) will have 20 percent of its individuals damaged to this degree. The remaining 90 percent of the plant population will be damaged likewise, but assume that only 1 percent of these plants have a chance of surviving (i.e., those growing where a tree *will* fall). With respect to natural selection, the selective pressure for a defense trait that will repel the caterpillar is generated by 50 percent herbivory of 20 percent of 10.9 percent of the individuals, while the amount of leaf eaten by the caterpillar population is 50 percent of 20 percent of 100 percent of the individuals. In short, enough leaf material to sustain a species of caterpillar may be harvested with only the amount of impact that would have been generated by a much less voracious species of caterpillar feeding on a plant population with a high proportion of individuals with a high chance of attaining their potential fitness. Alternatively, if the incoming caterpillar fed only on individuals with a high chance of surviving, it would have the same impact with much less herbivory that it would have if it also included ill-fated conspecifics in its diet. This scenario may also be stated as, "The more the caterpillar population is focused on ill-fated plants, the more likely it is to persist." At the limit, the caterpillar feeding on shed leaves is totally free of evolutionary responses by the plant to its feeding. Likewise, as the percentage of the plant population made up of ill-fated plants rises, there is a rise in the amount of herbivore load that will be sustained free of selective charge if the herbivores are distributed at random or focused on the ill-fated plants.

Two kinds of ecological complexity should be added to this hypothesized process. First, if the herbivory raises the probability that a plant will die before reproduction or that it will be a less prolific reproducer, there is the complication that the same amount of herbivory is likely to lower the realized fitness of a weakened plant more than that of a healthy one. This differential response may alleviate some of the ill-fated plant effect (eliminate some of the free ride) by rendering the herbivore less of a detritivore and more of a predator or parasite.

Second, while the herbivore subsisting largely or totally on ill-fated plants may not be selecting for traits to repel itself even if this leads to earlier plant death than would otherwise have occurred, it will still be ecologically thinning out its host plants. Furthermore, it will have to survive despite the defenses selected for by other more fitness-reducing species of herbivores, just as must the more conventional detritivores consuming litter.

It is critical to recognize that the selective process that may result in a larger herbivore load on ill-fated individuals or in larger herbivore loads on species that normally have a high proportion of ill-fated individuals does not favor local mutant herbivores for this trait per se. The individual herbivore that feeds on an ill-fated plant in preference to a plant with high potential fitness does not raise its own fitness. Rather, the selective process is that of the plant suffering or repelling herbivores that are serendipitously arriving through the evolution of other traits or by immigration.

What fraction of the leaf-eating herbivores in Santa Rosa habitats are largely supported by ill-fated plants with little or no potential fitness? Furthermore, what proportion of the herbivores subsists on ill-fated plants because those plants were actively sought by ovipositing females or because their habitats are so sought? In both cases, I assume that the selection for this choice was not driven by a selective value to the individual female ovipositing on the plant with a low potential fitness. It is easy to imagine that many of the Santa Rosa seed predators subsist on seeds that have zero fitness because of their site of deposition following dispersal (or lack thereof). It is much more difficult to divine the potential fitness of the young growing plants whose leaves are important food for so many caterpillars at Santa Rosa. There certainly are many species of caterpillars at Santa Rosa that wholly or largely feed on saplings of forest canopy trees in the deeply shaded understory where the host has virtually no chance of survival to reproduction unless a tree fall occurs at that site. I cannot yet offer data on the influence of this herbivory on how long a plant can wait before finally dying of starvation, distorted stems, disease, etc.

## CLIMATE IS A HOST-PLANT TRAIT

The physical environment undoubtedly influences caterpillar fitness. We tend to forget that each local population of plants, and even distinctive subsets of the population, is associated with a distinctive microclimate. The caterpillar has to contend with this as much as with the directly genetically programmed traits of the plant and the plant's distinctive carnivory regime. Variation in this climatic regime over a plant's distribution may as well as responsible for the absence of a caterpillar in parts of the plant's range as is geographic variation in host plant chemistry. That the saturniid moth *Schausiella santarosensis* is apparently found only in northwestern Guanacaste Province, Costa Rica, while its host tree, *Hymenaea courbaril*, ranges from southern Mexico to central South America, could have many causes besides local uniqueness of *H. courbaril* chemistry. Among these causes may be the Santa Rosa climate.

At Santa Rosa, there are many examples of climatic components of what might be termed the suitability profile of caterpillar host plants. One that is annoyingly omnipresent is the failure of many species of saturniids to have at least the minimum of three generations per year that could occur if host foliage properties were the only challenge to the caterpillar. While in theory such failures may be equally attributable to seasonal change in carnivory risk or leaf chemistry, there are times when climate seems to be the likely primary cause.

The four saturniids that feed on the foliage of *H. courbaril* offer an example. This tree bears resin-rich leaves (e.g., Langenheim et al. 1982) throughout the year, except for approximately 2 weeks in December or January (early dry season) when the old leaf crop is dropped and a new one is put out immediately thereafter. All four species of saturniids that eat *H. courbaril* leaves can be reared readily under nets in the field or in plastic bags in the laboratory on foliage collected at any time of year (unpublished field notes).

*H. courbaril* foliage of all ages is eaten by all four species in nature and in the laboratory. Throughout the dry season, from at least January until shortly before the first rains in late April or early May, three of the four saturniids are dormant in cocoons or as pupae in the litter below the fully leafed adult *H. courbaril*, and *Hylesia lineata* Drc. is dormant as eggs in an arboreal felt nest constructed by the female (Janzen 1984a). *Dirphia avia* anticipates the rains and times its emergence so that ovipositing females are in the forest as much as a week before the rains. The eggs require 2–3 weeks to hatch, with the consequence that the caterpillars begin feeding during the rains. *Schausiella santarosensis, Periphoba arcaei* (Drc.), and *Automeris zugana* Drc. adults emerge within 3 weeks after the first heavy rains, and their first-generation caterpillars are present for the first 2–3 months after the rains begin. *H. lineata* eggs hatch shortly after the rains begin as well, with the same consequence. Most of the pupae of the first generation of *S. santarosensis* remain dormant in the variably wet and dry litter below the *H. courbaril* for 9–10 months before eclosing to repeat the process the next year; however, a small fraction of these pupae eclose about 3 weeks after pupation and constitute a second generation during the second half of the rainy season. This latter generation again demonstrates that the leaves of *H. courbaril* are chemically quite suitable as food for *S. santarosensis* at this time of year. The pupae of this second generation then join those of the first generation in remaining dormant below the leafy trees throughout the dry season. The other three saturniids regularly have two generations on the rainy season *H. courbaril* leaf crop (as well as on other species of hosts) and then become dormant at the end of the rainy season. It is hard to avoid the working hypothesis that the reason that these moths ignore a food source on which they could pass at least two more generations is because the dry season heat and wind, and attendant desiccation, are inimical to their development in the crown of a large tree. The first-instar larvae are probably the most susceptible, but desiccation during molting and even during pupal formation may also be a problem.

Larval mortality from desiccation will probably turn out to be a major reason for delaying oviposition until the rains start, even when the host plant is in full leaf. For example, at the beginning of the 1983 rainy season (late May), there was sufficient rain to cause some *Cochlospermum vitifolium* to leaf out. This plant is a natural host of *Eacles imperialis* (Table 2). I placed hundreds of 1-day-old first-instar *E. imperialis* larvae on these leafy *C. vitifolium*. The plants were then naturally subject to winds, high temperatures, direct insolation, and dry air as severe as was characteristic of midday a few weeks earlier during the dry season. It was dry enough to stop further *Cochlospermum* branch elongation. While the caterpillars did feed, few obtained enough water to replace that lost by desiccation, and I watched them quite literally dry up and blow off during the following 2 days. Two weeks later, after rainy season humidity, cloudiness, and still air had set in, similar inoculations of the same plants resulted in nearly 100-percent larval survival (the larvae were protected from carnivores with netting in these experiments). The same change occurred with *Rothschildia lebeau* first-instar larvae put on insolated sapling *Spondias mombin* during the same days. For both species, the foliage of their host plants during the dry weather was excellent fodder when given to siblings of the dead caterpillars in plastic bags in the laboratory.

In short, at the beginning of the rather erratic 1983 rainy season, the leaves of major host plants of *E. imperialis* and *R. lebeau* were present and edible but, in effect, unavailable. In addition, there was spatial heterogeneity to their availability. Inoculation experiments, using siblings of the victims at the beginning of the rainy season, were quite successful when the young caterpillars were placed on host plants that happened to be growing in the shade and wind-buffered air of a patch of evergreen trees. Had these shaded plants been of a different species, one of the other host species of these two moths, it would be easy to conclude that these ecologically available species of host plants had different weather regimes from those of *C. vitifolium* and *S. mombin*, thereby giving them a longer period of susceptibility to the caterpillars during the year. It is likewise easy to imagine that this different regime might well make them an acceptable host for a species of caterpillar that has no other species of host in the habitat.

The weather becomes a trait of the host plant in more ways than just its direct effect on the caterpillar. By determining the duration of leafiness, the weather determines such things as the number of caterpillar generations possible. This may in turn determine the length of a generation, because the number of generations per rainy season must be an integral number. The length of a generation may in turn determine which hosts are too good and which are inadequate. An inadequate host may be one that the caterpillar can eat with impunity, yet lacks sufficient nutrients for the caterpillar to attain a reasonable size by the time it must pupate if it is to remain in synchrony with the remainder of its population. A too-good host might be one that makes the caterpillar grow too fast; however, in this case, I would expect quick selection for a fixed larval period coupled with heavier caterpillars on better host species or individuals. Viewed the other way around, a given nutrient and defensive chemistry may generate a moth egg-to-adult cycle that is incompatible with the seasonality of the site even if the resultant adult moths are quite normal in weight and other physiological paramenters.

## DISCUSSION

A host plant is not the focus of the ecological and selective regime of a moth and its caterpillars. Rather, the focus is a space bounded by parameters involving carnivores, climate, host chemistry, host fitness depression through herbivory, and a variety of other traits. In a certain sense I am defining a Hutchinsonian niche for a caterpillar and arguing that this niche is not centered on any one of these traits. This notion is emphasized by recognizing that in any particular point in season, space, or ontogeny there are many individuals of the caterpillar's host plant population that are not being fed on by that species of caterpillar; this distribution is not necessarily generated by randomly placed misses, but because of predictable caterpillar failure or disinterest under this or that circumstance. A particular host is necessary, but not sufficient, for caterpillar presence.

But is it even necessary? Why not eat just any plant? The current answer, and I am sure the largely correct one, is that in any given snapshot in evolutionary time, a caterpillar species is genetically (and subsequently, ecologically as well) programmed so that it feeds on only a few species of plants in the habitat; female oviposition behavior is here viewed as merely an extension of caterpillar behavior. However, there are at least two ways in which this answer is probably incomplete. First, and I think this is generally accepted by students of animal-plant interactions, there are probably more species of plants in the habitat that can be physiologically processed by the caterpillar species than the caterpillar species actually eats in nature. I have discussed here some of the reasons why these plants may not be used as hosts; the physical climate, predators, etc., may stop the evolution of the choice of that plant, and current ecological processes may prevent its use even if it is chosen by the ovipositing female. Second, given the right collection of ecological circumstances, perhaps just about any plant would be a suitable host in ecological time and certainly in evolutionary time.

In other words, is it unthinkable that, if a species of moth were confronted with a habitat rich in plant species but quite lacking in carnivores (including diseases), inclement weather, competitors, and the ability of plants to evolve further, it might well evolve a digestive physiology such that any individual caterpillar could feed on many or even all plant species? We can imagine that the genetic programming might be too complex and that the biochemical machinery somewhat incompatible for a caterpillar to contain all the collective food-processing abilities of the several thousand species of caterpillars now feeding on the plants of Santa Rosa. But what if, instead, the caterpillar simply developed a series of biochemical filters that, albeit slowly and incompletely, simply extracted the easily removed nutrients from the food and passed the rest on out? At Santa Rosa, *Hypercompe icasia* Cram. (Arctiidae) has over 60 species of broadleafed host plants recorded for it to date (in half as many plant families) and is one of the most slow-growing caterpillars I have ever reared. The sympatric *H. suffusa* Schaus has more than 50 recorded hosts, and there is almost no overlap of its host list with that of *H. icasia*; it not only grows very slowly, but if the food dries up, it spins a flimsy silk nest and waits until more green leaves appear. It can wait as long as 3 months at ambient temperatures. Why do most other Santa Rosa caterpillars appear to lack such digestive abilities? I doubt that it is because *Hypercompe* has invented some miraculous digestive system never hit upon by other Lepidoptera. I view *Hypercompe* not as the epitome of anything, but simply one of many ways to cope with the wide variety of selective and ecological pressures that confront a caterpillar.

I have mentioned quite enough complications in this essay that it seems truly a miracle for there to be any patterns at all. However, patterns do exist. The large moths at Santa Rosa – saturniids and sphingids – can be partitioned with respect to many of the traits mentioned here. I have already mentioned that sphingids are generally found in carnivore-rich mixes of small plants in low vegetation as well as in the crowns of large trees, while saturniids are much more caterpillars of the crowns of large trees. Sphingids rely heavily on crypsis specific to the host plant (or even leave the host plant during the day), while saturniids have both ostentatious real defenses and mimicry in addition to a more generalized crypsis. Closely linked to this contrast, sphingid caterpillars are more host-specific than are saturniids and grow faster than do saturniids.

On the one hand, it is nothing new to stress that a host plant is more than just its chemistry. But the topic needs stress now for two reasons. First, most analyses of nonchemical traits (e.g., plant apparency, size of the plant, or plant population as an island) have examined them as large-scale attributes, with the stress being on how these traits correlate with some caricature of host plant chemistry or numbers of insect species (e.g., Southwood et al. 1982). Such analyses are an essential part of the story but bypass the fine-scale interactions between species and individuals (e.g., Karban and Ricklefs 1983; Lawton 1982; Rausher and Papaj 1983; Connor et al. 1983) and the small-scale nonchemical traits. The nonchemical traits deserve the same detailed attention as specificity determinants that secondary compound chemistry is now receiving. Second, the topic needs stress because of the inherent difficulty in the technology of the subject. One cannot determine a caterpillar's risk of being eaten, for example, from any intrinsic trait of the plant (or the caterpillar) that can be obtained from laboratory analyses of collected materials. Equally, the depression of host plant fitness by a caterpillar population cannot be determined from any compilation of facts about plant species, including vegetation analyses, percentage of herbivory, percentage of cover, and all those other things traditionally measured. These traits are situation dependent. They have meaning only in context.

Here it is appropriate to digress on the subject of the concept of average or baseline herbivory. Plants live a long time. Grant proposals are for 3 or fewer years, and field studies are rarely more than one to two times this duration. A commonplace herbivory regime is small amounts for a run of years, with severe defoliation occurring at long and irregular intervals. Since severe defoliation events are sufficiently far apart that any one study usually sees none or only one of them, there is a strong temptation to view them as "unusual" and therefore not to be considered in determining the intensity of herbivory. While it does not make biological sense to *average* the years of peak herbivory with the many more years of much lower herbivory, somehow the impact of the plant's lifelong herbivory regime needs to be taken to be the same norm.

In characterizing the entire herbivory regime with its causes for variation, one finds that many of the nonchemical traits of the plant take on great importance. Leaving aside herbivore-induced changes in chemistry (e.g., Edwards & Wratten 1983), the defense chemistry and nutrients in a particular set of leaves are relatively invariant as causes of herbivory fluctuation when compared with other traits. Most of the individual caterpillars that actually attempt to feed on a given species of plant either can or cannot do it. And if they can, they can do it over much or all of a plant's lifespan. It is easy to forget that much of a plant's herbivore defenses are against those animals that, because of these defenses, are virtually never responsible for any leaf loss. We are in the silly situation that much of the study of secondary compound chemical ecology occurs in the vacuum of having no idea what herbivores selected for the defenses, and the intensity of much of the herbivory we measure is determined and patterned by events generally not measured by ecologists that study herbivory. The ultimate irony is that just as in the defense budgets of nations, the largest cost levied by herbivores is probably the cost of the defenses rather than the amount of material removed during herbivory (Janzen 1983b).

I have argued that a multispecies mix of small plants has a very different carnivory regime than does an equal-sized large tree crown, which is essentially a monospecific stand. For almost all biologists, the closest approximation of the multispecies mix of small plants is roadside and old field secondary succession. Such habitats are often analogized with natural disturbance sites such as tree falls, river banks, landslides, etc. I would only emphasize that the analogy is not a close one and likely to be particularly deceptive with respect to the case at hand. For example, the old field does not have nearby intact forest as an herbivore reservoir, refuge, and barrier between small portions of the old field. Likewise, tropical roadsides are, for example, generally continually bathed in dust, which is one of the best contact pesticides known (especially for small insects like parasitoids). For example, the only reason that the *Syssphinx molina* experiments mentioned earlier could be conducted was that they were conducted along a rarely traveled paved road with no shoulders.

It is clear that any herbivore entering a new habitat is stepping into a battlefield rich in plant defenses selected for by other herbivores and by the constraints of defense economics. This situation applies even more to the nonchemical traits of a host plant, the traits I have been discussing; many of the traits of importance were not even selected for by biotic agents, to say nothing of herbivores. The opportunities for coevolution have been minimal. The traits that render a *Hymenaea courbaril* crown a low-yield area for a carnivore were certainly not selected for by the four saturniid caterpillars that feed with relative impunity on the leaves in large *H. courbaril* crowns. It is unlikely that host leaf colors, shapes, and sizes, are selected for through their rendering caterpillars of a particular species easily found by carnivores.

Unfortunately for evolutionary ecology, it is at least theoretically possible for natural processes to produce a habitat full of interacting caterpillars and their hosts with no coevolution and even very little (if any) evolution. This is particularly true for the nonchemical traits of plants. One can imagine an arriving caterpillar finding a number of edible species of plants but ending up using only a small fraction of the species and biomass because of the negative effects of processes like those mentioned in this essay. Whether the caterpillar persists until it is evolutionarily modified by the many new selective pressures put upon it should depend largely upon nonchemical factors, if there is even one species of plant present that the caterpillar can eat.

The immigration placement of a caterpillar in a new habitat, and its ecological adjustment to the plants there, has much in common with the process of the introduction of new pollinators, new dispersal agents, animal-dispersed plants, etc. At first, the persistence of the invader (or a resident newly deprived of its interactant) depends on other organisms with traits similar to those of the organisms it left behind, even if the invader cannot achieve the same level of fitness that it had originally. At least theoretically, the interactions could then continue indefinitely with no evolution – though the population structure of the incoming species might be quite different than it was where it came from (as might also be those of its new associates). In fact, it is easy to imagine a species being passed from interactant to interactant over long evolutionary time, with a truly new phenotype appearing only rarely but with largely the same phenotypes of organisms continuing to interact in this or that habitat (e.g., Janzen 1983c). Perhaps evolutionary rates proceed most rapidly where species richness is lowest, since in such a situation the probability that alternate or substitute interactants are present is lowest. Yet, there has to be enough diversity of substrate for the immigrant at least to get established. At the other extreme, if there are many similar species in a habitat, the addition of one more may result in virtually no discernible evolutionary change, because each of the ecologically similar species adjusts just a small amount.

## SUMMARY

To the herbivore evolutionarily moving onto a host, or surviving there, a host plant has, in addition to its chemistry and other personal traits, a carnivore regime, weather regime, and fitness regime that must be overcome by the herbivore. The interplant heterogeneity of a Costa Rican defoliation of *Randia* treelets by *Aellopos titan* sphingid caterpillars is described as due to heterogeneity in the carnivory regime rather than in the interplant chemistry. That Costa Rican saturniid caterpillars feed primarily in the crowns of large trees while in the same habitat sphingid caterpillars are distributed over many more plant life forms and sizes is attributed to saturniids (except the severely urticating species) being comparatively incompetent at contending with the more intense carnivory regime of dense, low, and plant-species-rich vegetation rather than to saplings having different foliar chemistry than have their large parents. The saturniid phenology of there not being caterpillars on evergreen trees during the dry season in the same forest is ascribed to desiccation during this time of year rather than to different leaf chemistry in the dry season. Finally, I argue that the impact of herbivory, and hence the likelihood that it will select for defense traits against a herbivore, is related to the potential fitness of the actual plants fed upon. A plant that is slated

to die for other reasons is evolutionarily dead even if physiologically living; the accumulation, over evolutionary time, of an herbivore load by ecologically distinctive conspecifics of different potential fitness should differ with that potential fitness. Furthermore, the accumulation of an herbivore load by a species of plant may well be influenced by the proportion of the population of growing juveniles that are in the category of "evolutionarily dead."

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# Plant Kairomones and Insect Pest Control

Robert L. Metcalf

*"There can be hardly an entomologist today who does not know that host selection is the very heart of agricultural entomology and that secondary plant substances are the clues to the problem." — G. Fraenkel (1969)*

*"The extraordinary variety of insect plant relationships is likely to be based on more diverse mechanisms than can be foreseen at present. The promise of rewards is rich for investigators who approach the problem free of deeply rooted bias." — A. J. Thorsteinson (1960)*

Estimates suggest that there are at least 100,000 chemical compounds produced during the growth and development of the more than 200,000 species of flowering (vascular) plants (Harborne 1982). The vast majority of these chemicals are the so-called "secondary plant compounds," not essential for the normal physiology of the plants, but rather the seemingly capricious outpourings of nature's chemical factories, the alcohols, esters, ketones, terpenoids, steroids, alkaloids, flavonoids, phenylpropanoids. It is only when we examine carefully the evolutionary processes that have brought about the diversification and speciation of plants that this enormous array of organic chemicals takes on purposeful and orderly significance.

The external plant environment is pervaded by these compounds of secondary metabolism that ooze from leaves, blossoms, and fruits. While humans are well aware of many of them because they define the colors, odors, and tastes that characterize our interactions with plants, there are countless others, less conspicuous in either quality or quantity, that dominate the lives of the 500,000 or so species of insects that have coevolved with the flowering plants. Many of these allelochemicals generate olfactory or gustatory stimuli that convey behavioral messages to species involved in the coevolutionary and ecological interrelations of food webs. From an arthropogenic point of view these allelochemics are perceived by insect sensory receptors as attractants, repellents, or arrestants, and in a more complex way, as antibiotics that disrupt normal growth, development, fecundity, and longevity or as antixenotics that disrupt normal host selection processes. From the viewpoint of the processes of coevolution between plants and insects, these allelochemics are classified as *allomones* if they convey adaptive advantage to the plant producer and as *kairomones* if they convey adaptive advantage to the insect receiver (Kogan 1983).

Fraenkel (1959) reviewed much of the early history of our understanding of the reasons for the existence of plant allelochemics and suggested the criteria for their positive identification as isolation and identification of the chemical, initiation of the kairomone or allomone response when applied to a neutral surface, and demonstration of a quantitative relationship between the concentration of the allelochemic and the insect response. The same chemical compound may act as an allomone, protecting the plant against some herbivores, and as a kairomone, stimulating the feeding of other herbivores, depending upon the vagaries of mutations and coevolution. Specific kairomones may be formed by a wide variety of plant families, and thus, these kairomones may be attractive to particular insect pests that exhibit a wide host range.

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## Coevolution of Plants and Insects

The coevolutionary history of the plant kingdom with the insect world is an important area of investigation for both fundamental and applied studies in entomology. The relatively enormous numbers of species involved, some 500,000 insects and 200,000 plants, and the vast expanse of more than 300 million years of evolutionary time concerned, serve not only to provide almost unlimited examples of plant-insect interactions for study, but also have obscured many of the key interrelationships in the mists of time. Some of the salient history, as recorded in the fossil records, is portrayed in Fig. 1. The first land plants are thought to have appeared about 420 million years ago in the Devonian Period, and the first flowering plants occurred about 225 million years ago in the Triassic Period. These preceded the appearance of fruits in the Cretaceous Period, little more than 100 million years ago. This segment of evolutionary time was overlapped by the evolution of the Insecta, which evolved about 300 million years ago in the Carboniferous Period and were well diversified into modern orders by the Permian Period 270 million years ago (Riek 1970). The first fossil records of insect-damaged leaves are found in the Permian Period.

These relationships between plants, chemicals, and insects are seminal in understanding speciation, coevolution, zoogeography, ecology, and insect behavior, and they are of primary importance in the applied ecology of host-plant susceptibility and resistance to insect attack. In this review we will consider two groups of insects that have exploited plant kairomones so that some of their species have become dominant pests of agriculture. The principal thesis explored is that insect response to plant-produced kairomones is largely a function of specific kairomone receptor organs on antennae, palpi, or tarsi that have active sites structurally complemen-

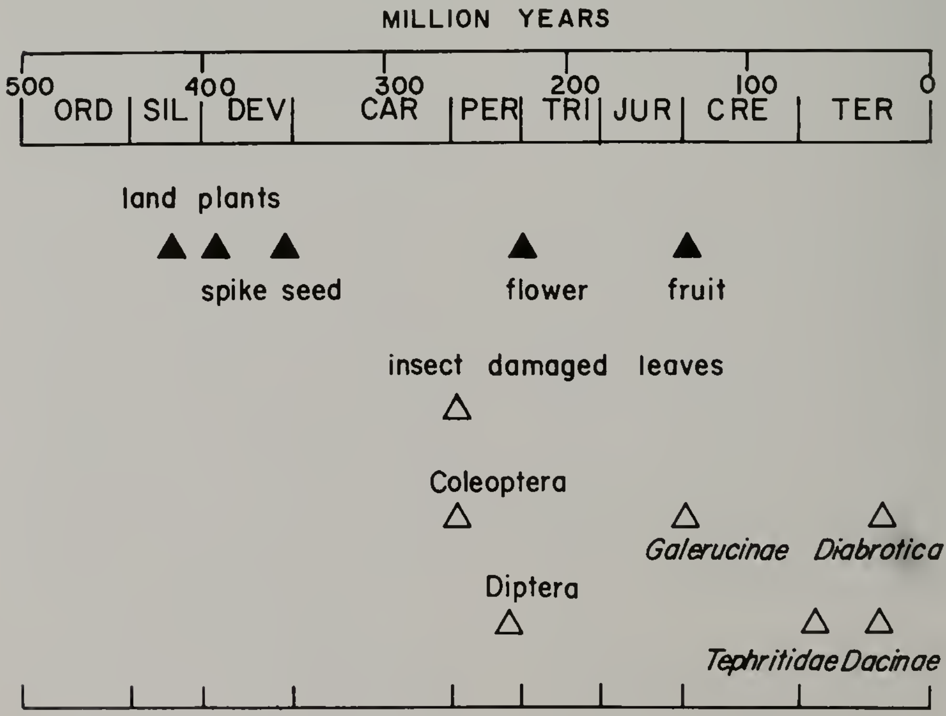

Fig. 1. – Coevolution of plants and insects. (Smart & Hughes 1973 and Riek 1970).

tary in conformation to the structures of the kairomones. The specific kairomone receptor is the product of millions of years of coevolution between host plant and insect pest and has been gradually modified by successive mutations that have provided the insect with adaptive advantages in terms of previously inaccessible ecological niches. As plant allelochemics have become more and more diversified, insect kairomone receptors have become shaped to accommodate them.

## PHENYLPROPANOIDS IN COEVOLUTION OF THE DACINI

The fruitflies of the tribe Dacini (order Diptera, family Tephritidae) constitute a closely related and rapidly evolving group of more than 1,000 species found in the Old-World tropics (D. E. Hardy, University of Hawaii, personal communication). The female flies have sharp piercing ovipositors and typically insert their eggs into a wide variety of fruits and vegetables in which the larvae develop. Many of the Dacinae are remarkable for their wide host range: *Dacus dorsalis* Hendel, the oriental fruitfly, has been reared from more than 150 plants, and *D. tyroni* (Froggatt), the Queensland fruitfly, from more than 106 hosts (May 1953). *D. cucurbitae* (Coquillett) the melon fly, has been recorded as attacking more than 40 different kinds of plants in 12 families, including melons, cucumbers, squash, gourds, tomatoes, and peppers (Hardy 1949). Many other species of this subfamily are much more restricted in host range (Allwood & Angeles 1979), and the host plant preferences for the majority of species seem not to be recorded.

Howlett (1912, 1915) first reported that citronella oil was attractive to the male fruitflies, *Dacus diversus* Coquillett and *D. zonatus* (Saunders), in India and subsequently demonstrated that 3,4-dimethoxyallylbenzene, or methyl eugenol, a constituent of citronella oil, was highly attractive to males of these flies and of *D. dorsalis* (=*D. ferrugineus* (Fabricius).

*D. cucurbitae* males were shown to be highly attracted to 4-(*p*-methoxyphenyl)-2-butanone, or anisyl acetone (Barthel et al. 1957), and 4-(*p*-acetoxyphenyl)-2-butanone, or cue-lure, was developed subsequently as a more effective lure (Beroza et al. 1960). Cue-lure is intrinsically less attractive than its hydrolysis product, 4-(*p*-hydroxyphenyl)-2-butanone, raspberry ketone or Willison's lure (Kaiser et al. 1973; Drew 1974), a natural product first isolated from the raspberry (Schinz & Seidel 1961).

Drew and his coworkers, in a monumental series of trapping experiments in Australia and New Guinea, have surveyed the response of more than 150 species of the tribe Dacini to methyl eugenol and to cue-lure or raspberry ketone (Drew 1974; Drew et al. 1981; Drew & Hooper 1981). From their data and those of others (see *Review of Applied Entomology*), it appears that approximately 90 species of Dacini have been shown to respond to cue-lure or raspberry ketone and 40 species to methyl eugenol. No species has been shown to respond to both types of lure, and all species within each complex of closely related species responded to the same lure, indicating that the olfactory response has profound evolutionary implications. Hardy (1979) estimates that 90 percent of all Dacini respond to one or the other of these lures.

Both methyl eugenol and raspberry ketone are phenylpropanoid secondary plant compounds derived during plant evolution from phenylalanine through a common precursor, *p*-hydroxycinnamic acid or *p*-coumaric acid (Geissman & Crout 1969; Friederich 1976), as suggested in Figure 2. It appears that an ancestral Dacini in Southeast Asia must have developed an association with rotting fruits containing coumaric acid and that this compound became a kairomone regulating early Dacini behavior. The Tephritidae are believed to have arisen in the Paleocene era about 65 million years ago (Fig. 1).

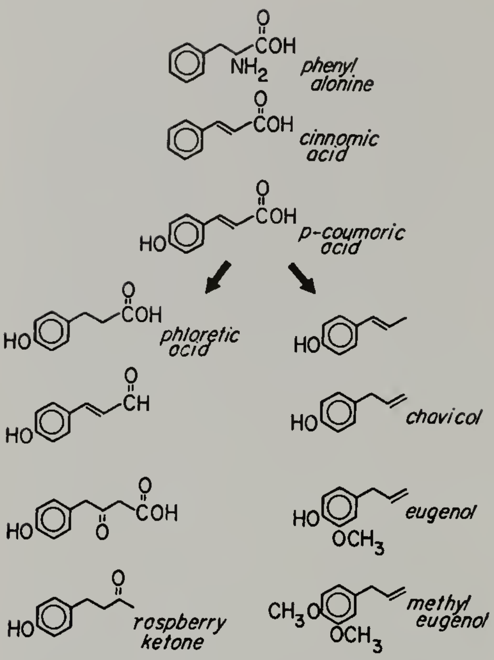

Fig. 2. – Plant evolution of phenylpropanoids from phenyl alanine. Arrows indicate divergence leading to the development of kairomones for two distinct groups of Dacini.

Both methyl eugenol for *D. dorsalis* and raspberry ketone for *D. cucurbitae* are attractive in nanogram quantities on filter paper, and *D. dorsalis* has been shown to respond by attraction, orientation, and feeding to as little as 100 pg of $^3$H methyl eugenol present on the antennae where the olfactory receptors are located (Metcalf et al. 1981). Thus, the sensitivity of the responses of these fruitflies to these two kairomones approaches that of various male lepidoptera to the female sex pheromones. However, in contrast to the very precise stereochemical conformity between sex pheromone and receptor (Blum et al. 1971; Priesner et al. 1975), the kairomone receptors of both *D. dorsalis* and *D. cucurbitae* are responsive over a range of about $10^8$ in concentration and to a wide variety of organic chemicals with structural resemblances to methyl eugenol or to raspberry ketone (Metcalf et al. 1975, 1979, 1981, 1983b) (Table 1). The male Dacini respond to odorant compounds by a characteristic behavioral sequence of a) orientation, b) searching, c) arrest, and d) compulsive feeding (Metcalf et al. 1979) that is highly reproducible. The degree of complementarity or "fit" of individual odorants to the kairomone receptors on the male Dacini antennae can be judged by determining the least amount of odorant, applied to filter paper under standardized conditions and exposed to fruitfly populations of uniform age, that produces the behavioral sequence. This value is termed the limit of response (LR) (Metcalf et al. 1979, 1983).

Methyl eugenol is widely distributed in plants, and there are numerous recorded observations of male Dacini aggregating and feeding on plant sources, as shown in Table 1. Phloretic acid has recently been found in the blossoms of *Cucurbita pepo* Linnaeus (Itokawa et al. 1983), and its presence may account for the association of at least 10 species of Dacini, including the melon fly *Dacus cucurbitae*, with various Cucurbitaceae.

## KAIROMONE RECEPTOR INTERACTIONS IN THE DACINI

The sensory receptor organs that trigger the responses of male Dacini to the phenylpropanoids are located on the scape of the antenna, and bilateral antennectomy abolishes the response (Metcalf et al. 1975). The antennal receptors, as revealed by scanning electron microscopy, are typical *sensilla basiconica*. The most notable feature of the Dacini response to phenylpropanoid kairomones is the sharp demarcation of the tribe Dacini into species responding to 4-(*p*-hydroxyphenyl)-2-butanone, or raspberry ketone, and its close analogues, e.g., *Dacus cucurbitae*, the melon fly, and species responding to 3,4-dimethoxyallylbenzene, or methyl eugenol, and its close analogues, e.g., *Dacus dorsalis* (Drew 1974; Drew & Hooper 1981).

The data in Table 2 show the sensitivity of response (LR) of these two key

Table 1. — Plants containing methyl eugenol to which male Dacini are attracted.[a]

| Family | Plant Species | *Dacus* Species |
|---|---|---|
| Anacardiaceae | *Mangifera indica* Linnaeus (mango flower) | *D. diversus* Coquillett, *D. correctus* (Bezzi) |
| Araceae | *Colocasia antiquorum* Schott | *D. dorsalis* Hendel, *D. zonatus* (Saunders) |
| Bromeliaceae | *Vriesea heliconioides* (Humboldt, Bonpland & Kunth) Hooker ex Walpers (blossom) | *D. dorsalis* |
| Caricaceae | *Carica papaya* Linnaeus (papaya flower) | *D. dorsalis*, *D. diversus* |
| Labiatae | *Ocimum basilicum* Linnaeus | *D. dorsalis* |
| | *O. sanctum* Linnaeus (tulsi) | *D. correctus* |
| Lecythidaceae | *Couroupita guianensis* Aublet (cannon-ball tree, blossom) | *D. dorsalis* |
| Leguminosae | *Cassia fistula* Linnaeus (golden shower tree, blossom) | *D. dorsalis* |
| Myrtaceae | *Pimenta racemosa* (Miller) J. W. Moore | *D. diversus*, *D. dorsalis*, *D. zonatus* |
| | *Syzygium cumini* (Linnaeus) Skeels (= *Eugenia jambolana*) (jamum tree) | *D. caudatus*, *D. diversus*, *D. dorsalis*, *D. zonatus* |
| | *S. aromaticum* (Linnaeus) Merrill & L. M. Perry (= *Eugenia aromaticum*) (clove) | *D. zonatus* |
| Piutaceae | *Pelea anisata* Mann (leaf, twig) | *D. dorsalis* |
| | *Zieria smithii* Andrews (leaf) | *D. cacuminatus* (Hering) |
| Saxifragaceae | *Brexia madagascariensis* (Lamarck) Noronha (blossom) | *D. dorsalis* |

[a] Howlett (1915), Kawano et al. (1968), Metcalf et al. (1975), Fletcher et al. (1975), Shah & Patel (1976).

species to a variety of phenylpropanoids and related compounds (Metcalf et al. 1983b). It is evident that *D. cucurbitae* shows maximum response to phenylpropanoids with a *p*-OH group on the phenyl ring and a C=0 group about 2 atomic diameters removed from the phenyl ring, as typified by raspberry ketone and methyl phloretate (see Fig. 2). *D. dorsalis* shows maximum response to phenylpropanoids with *m*- and *p*-$CH_30$ groups on the phenyl ring and a side chain with an unsaturated double bond, as typified by methyl eugenol and methyl isoeugenol. Neither species responded appreciably to the most effective odorants for the other species. The antennal receptors of *D. cucurbitae* and *D. dorsalis* must provide maximum structural complementarity to the kairomones which promote maximum attraction and feeding stimulation, raspberry ketone for *D. cucurbitae* and methyl eugenol with *D. dorsalis*. The degree of structural overlap between the two types of receptors is minimal, as shown in Table 2.

Present-day understanding of the evolution of phenylpropanoid synthesis in the plant kingdom indicates phenylalanine as a precursor and *p*-hydroxycinnamic acid (*p*-coumaric acid) as the common ancestral substance from which there was divergence to the eugenol-methyl eugenol and to the raspberry ketone-phloretic acid phenylpropanoids pathways (see Fig. 2) (Friedrich 1976; Metcalf et al. 1979, 1983b).

Table 2. — Limit of response (LR) of *Dacus cucurbitae* and *D. dorsalis* to kairomone analogues.[a]

| | LR in Micrograms | |
|---|---|---|
| | *D. cucurbitae* | *D. dorsalis* |
| 4-$HOC_6H_4CH_2CH_2C(O)CH_3$[b] | 0.03 | > 1,000 |
| 4-$HOC_6H_4CH_2CH_2C(O)OCH_3$[d] | 0.01 | > 1,000 |
| 4-$HOC_6H_4CH_2OC(O)CH_3$ | 0.1 | 1,000 |
| 4-$HOC_6H_4CH_2C(O)OCH_3$ | 0.1 | 1,000 |
| 4-$HOC_6H_4CH{=}CHC(O)OH$[f] | 1,000 | > 10,000 |
| 4-$HOC_6H_4CH{=}CHC(O)OCH_3$[c] | 3 | > 10,000 |
| 4-$HOC_6H_4CH_2CH_2C(O)OH$[e] | 10 | > 10,000 |
| 4-$CH_3OC_6H_4CH_2OC(O)CH_3$ | 1.0 | 3,000 |
| 3-$CH_3OC_6H_4CH_2OC(O)CH_3$ | 3,000 | > 10,000 |
| 2-$CH_3OC_6H_4CH_2OC(O)CH_3$ | 10,000 | 3,000 |
| 4-$CH_3OC_6H_4CH{=}CHCH_3$ | 10,000 | 10 |
| 3,4-$(CH_3O)_2C_6H_3CH_2OC(O)CH_3$ | 10,000 | 10 |
| 3,4-$(CH_3O)_2C_6H_3CH_2CH_2C(O)OH$ | > 10,000 | 1,000 |
| 3,4-$(CH_3O)_2C_6H_3CH_2CH_2C(O)OCH_3$ | 10,000 | 3.0 |
| 3,4-$(CH_3O)_2C_6H_3CH_2CH{=}CH_2$[g] | 1,000 | 0.01 |
| 3,4-$CH_3O)_2C_6H_3CH_2CH_2C(O)OH$ | > 10,000 | 1,000 |
| 3,4-$CH_3O)_2C_6H_3CH_2CH_2C(O)OCH_3$ | 10,000 | 3.0 |
| 3,4-$CH_3O)_2C_6H_3CH{=}CHC(O)OH$ | > 10,000 | 1,000 |
| 3,4-$CH_3O)_2C_6H_3CH{=}CHC(O)OCH_3$ | 3,000 | 3.0 |

[a] Metcalf et al. 1983.

[b] raspberry ketone

[c] methyl coumarate

[d] methyl phloretate

[e] phloretic acid

[f] *p*-coumaric acid

[g] methyl eugenol

The positive response of *D. cucurbitae* to *p*-hydroxycinnamic acid and the lack of response by *D. dorsalis* suggest that the kairomone receptor in *D. cucurbitae* is the more primitive type and that this species and the others in the large group of more than 90 species known to respond to raspberry ketone are more closely related to the ancestral forms of Dacini that coevolved with plants containing cinnamic acid. With the evolutionary development of oxygenase enzymes in plants, *para*-hydroxylation of cinnamic acid to *p*-coumaric acid was a likely first step in kairomone transformation. Subsequently, the *p*-hydroxyphenylpropanoids were methoxylated to *p*-methoxy and still further oxygenated to form 3,4-dihydroxy, 3-methoxy-4-hydroxy and eventually 3,4-dimethoxyphenylpropanoids (Friedrich 1976; Hanson & Havir 1979). Then, as secondary plant compounds became more lipophilic through methylation and acetylation and were sequestered as essential oils, the antennal receptor site was modified to accept more lipophilic molecules, such as raspberry ketone and methyl phloretate (Metcalf et al. 1983b). *D. dorsalis* and the smaller group of related species responding to methyl eugenol apparently represent descendents of a mutant form whose antennal receptors developed complementarity to the 3,4-dimethoxyphenylpropanoids, thus opening up new ecological niches.

There is good evidence that the primary attractive site on the male *D. dorsalis* antennal receptor is complementary to the *p*-$CH_3O$ group of methyl eugenol (Metcalf et al. 1983). For this series of compounds there is a high degree of negative correlation between LR values for *D. dorsalis* and the $\pi$ value for octanol/water partition of the substituent side chain, demonstrating the lipophilic nature of the receptor (Metcalf et al. 1981).

### Chemical Ecology of Host Selection in the Dacini

The role of phenylpropanoid kairomones in the regulation of the behavioral ecology of the Dacini is complex. The lack of responsiveness of the females to these substances is puzzling. However, it appears that in the presence of male Dacini the kairomones can act as short-range ovipositional stimulants. The sex pheromones of the Dacini are produced in rectal glands of the males and attract virgin females. Thus, the plant kairomones may promote host selection by producing male aggregation and consequent sex pheromone release to bring females to suitable sites, where short-range ovipositional stimulation occurs (Metcalf et al. 1983b).

## CUCURBITACINS IN COEVOLUTION OF THE LUPERINI

The more than 300,000 described species of beetles of the order Coleoptera comprise nearly one-third of all insects and form the largest order of living organisms. The preponderance of species of Coleoptera feed on plants, and representatives first appeared about 260 million years ago in the Permian era (Fig. 1; Riek 1970).

The Chrysomelidae, or leaf beetles, (over 20,000 described species) feed almost exclusively on plants, and the coevolutionary association between plants of the family Cucurbitaceae and beetles of the tribe Luperini provides the most comprehensive example of the role of allelochemics acting as kairomones to promote host selection and feeding by phytophagous insects. The family Cucurbitaceae contains some 900 species of plants in about 100 genera, many familiar as the gourds, squash, cucumbers, and melons of *Cucurbita, Cucumis, Citrullus, Lagenaria, Marah, Sicyos, Echinocystis, Ecballium,* and *Bryonia.* At least 100 species in 30 genera of Cucurbitaceae have been shown to contain a group of more than 20 oxygenated tetracyclic triterpenoids, the cucurbitacins (Cucs) (Fig. 3). The Cucs are responsible for the characteristic bitter taste of most wild Cucurbitaceae (Rehm 1960; Lavie & Glotter 1971). Current thinking holds that the Cucs were selected by coevolutionary processes to protect the Cucurbitaceae against attack by a wide variety of both invertebrate and vertebrate herbivores. The Cucs are the most intensely bitter substances yet characterized and can be detected in aqueous solution at concentrations as low as 1 ppb (Metcalf et al. 1980). They are also extremely toxic, with intraperitoneal $LD_{50}$ values of Cuc A mouse 1.2, rat 2.0, Cuc B mouse 1.0 mg per kg (David & Vallance 1955). There have been instances of severe poisoning and death in sheep and cattle that consumed bitter *Cucumis* and *Cucurbita* fruits during drought conditions (Watt & Breyer-Brandwijk 1962). Very recently an epidemic of human illness in Australia resulted from the eating of zucchini-type *Cucurbita pepo* fruit that contained about 1 mg per g of Cucs (fresh weight), apparently as the result of a genetic reversion (Ferguson et al. 1983a). A number of insect pests, including the leaf beetles *Phyllotreta nemorum* (Linnaeus), *P. undulata* (Kutschera), *P. tetrastigma* (Comolli),

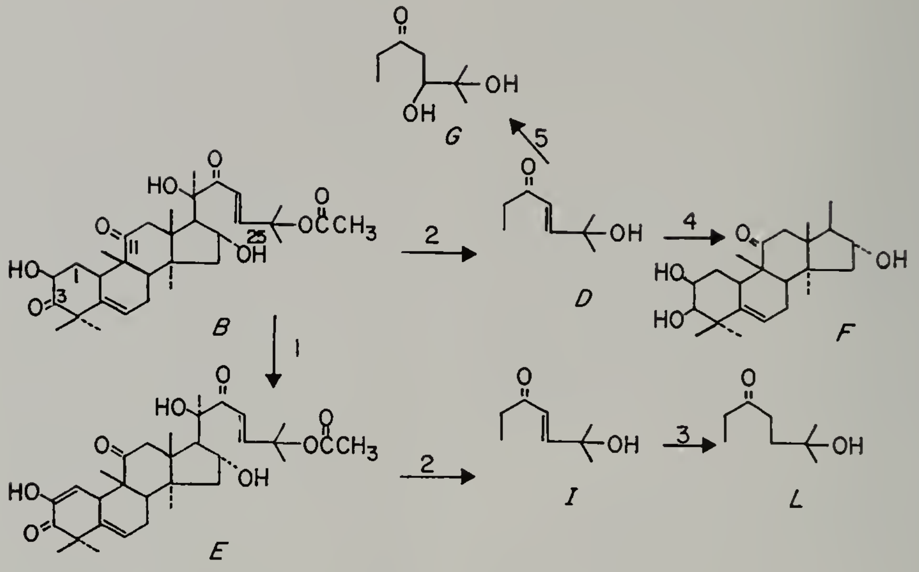

Fig. 3. – Suggested plant evolution of cucurbitacins B, E, D, I, F, G, and L. Numbers refer to specific enzymes involved: 1) cucurbitacin $\Delta^1$ dehydrogenase, 2) cucurbitacin acetylesterase, 3) cucurbitacin $\Delta^{23}$ reductase, 4) cucurbitacin C3-hydroxylase, and 5) cucurbitacin C24-hydroxylase (Lavie & Glotter 1971).

*Phaedon cochleariae* (Fabricius), *P. cruciferae* (Goeze), and *Cerotoma trifurcata* (Forester), are strongly deterred from feeding by the presence of Cucs (Nielson et al. 1977; Metcalf et al. 1980).

In contrast, the most important insect pests of Cucurbitaceae worldwide are found in a large group of beetles of the tribe Luperini, comprising 1,528 species of Old-World Aulacophorina (535 species) and the New-World Diabroticina (993 species) (Wilcox 1972). Luperini contains such destructive pests of cultivated crops as *Diabrotica undecimpunctata howardi* Barber, the spotted cucumber beetle or southern corn rootworm; *D. undecimpunctata undecimpunctata* Mannerheim, the western spotted cucumber beetle; *D. balteata* LeConte, the belted or banded cucumber beetle; *Acalymma vittatum* (Fabricius) and *A. trivittatum* (Mannerheim), the striped cucumber beetles; *D. barberi* (Smith and Lawrence), the northern corn rootworm; *D. virgifera virgifera* LeConte, the western corn rootworm; *D. virgifera zea* Kryson and Smith; *D. speciosa* Germar of South America; *Aulacophora foveicollis* of Asia, Africa, and Europe; and *A. femoralis* of Siberia, China, and Southeast Asia. The larvae of these beetles are rootworms, and the adults are found feeding on cucurbits, corn, beans, peppers, and a variety of other plants.

Host plant records are sorely lacking, and Wilcox (1972) in the authoritative *Coleopterorum Catalogus* lists only 29 for 1,528 species of Luperini; 72 percent of the records are for Cucurbitaceae. A literature search has disclosed 49 species, listed in Table 3, as feeding on Cucurbitaceae (e.g., Takizawa 1978). These 49 species represent more than 80 percent of the published host records for the Luperini and portray a relationship between these beetles and the Cucurbitaceae that is widely distributed between the Old-World Aulacophorina and the New-World Diabroticina. Compulsive feeding of the Luperini beetles on the leaves and fruits of wild, bitter Cucurbitaceae has been described for many of these species, and *Diabrotica balteata*, *D. barberi* (as *D. longicornis*),

Table 3. — Chrysomelidae: Galerucinae: Luperini Associated with Cucurbitaceae [a]

| Species | Plant Hosts | Locations |
|---|---|---|
| Aulacorphorina | | |
| Aulacophora | | |
| *A. abdominalis* (Fabricius) | cucumber, melons, pumpkin | Indonesia, Australia |
| *A. atripennis* (Fabricius) | gourds, pumpkin, muskmelon | Indonesia |
| *A. bicolor* (Weber) | wild, cultivated Cucurbitaceae | Taiwan, Indonesia, China, India, Japan, Phillipines |
| *A. cincta* (Fabricius) | snake gourd, bitter gourd, bottle gourd | India, Ceylon |
| *A. coffeae* (Hornstedt) | melons, pumpkin | Indonesia, Fiji |
| *A. excavata* Baly | *Citrullus, Cucumis, Cucurbita, Lufta* | India |
| *A. femoralis* (Motschulsky) | wild, cultivated Cucurbitaceae | Siberia, Japan, Phillipines, Viet Nam |
| *A. foveicollis* (Lucas) | pumpkin, squash, muskmelon | Asia, Africa, S. Europe |
| *A. hilaris* (Boisduval) | pumpkin, marrow | Australia, Micronesia |
| *A. lewisii* Baly | wild, cultivated Cucurbitaceae | S.E. Asia, Pacific Islands |
| *A. loochooensis* Chujo | Cucurbitaceae | Ryukyu Islands |
| *A. nigripennis nigrippennis* Motschulsky | squash, cucumber | Siberia, China, Japan, Korea, Taiwan |
| *A. n. nitidipennis* Chujo | Cucurbitaceae | Ryukyu Islands |
| *A. olivieri* Baly | melons, cucumber, pumpkins, squash | Australia |
| *A. quadrimaculata* (Fabricius) | *Citrullus lanatus* (Thunberg) Matsumura & Naki, *Cucurbita pepo* Linnaeus | Pacific Islands, Australia |
| *A similis* (Olivier) | *Citrullus lanatus, Cucumis melo* Linnaeus, *C. sativus* Linnaeus, *Cucurbita pepo* | S.E. Asia, Samoa, Fiji |
| Paridea | | |
| *P. angulicollis* (Motschulsky) | *Gymnostemma pentaphyllum* (Thunberg) Makino, *Trichosanthes cucumeroides* Maximowitz ex Franchet & Savatier | China, Japan, Taiwan |
| *P. costata* (Chujo) | wild Cucurbitaceae | China, Taiwan |
| *P. sauteri* (Chujo) | wild Cucurbitaceae | Taiwan |
| *P. sexmaculata* (Laboissiere) | wild Cucurbitaceae | Taiwan |
| *P. testacea* Gressit & Kimoto | wild Cucurbitaceae | China, Taiwan |
| Agetocera | | |
| *A. discedens* Weise | wild Cucurbitaceae | Taiwan |
| *A. taiwana* Chujo | wild Cucurbitaceae | Taiwan |
| Lamprocopa | | |
| *L. delata* (Erichson) | Cucurbitaceae | Ethiopia, Angola, Zambesi, Madagascar |
| Paragetocera | | |
| *P. involuta* Laboissiere | wild Cucurbitaceae | China, Tibet, Taiwan |
| Diabrotica | | |
| *D. balteata* Leconte | Cucurbitaceae cultivars | USA, Columbia, Venezuela, Cuba |

Table 3. — Continued

| Species | Plant Hosts | Locations |
|---|---|---|
| *D. cristata* (Harris) | Cucurbitaceae | Central USA |
| *D. longicornis* (Say) | *Cucurbita foetidissima* Humboldt, Bonpland & Kunth | Central USA |
| *D. graminea* Baly | | Costa Rica, West Indies, Cuba, Puerto Rico |
| *D. speciosa* (Germar) | *Cucurbita andreana* Naudin | Mexico to Argentina |
| *D. tibialis* Jacoby | Cucurbitaceae | S. Texas, Mexico |
| *D. virgifera* Leconte | *Cucurbita foetidissima* | Central USA |
| *D. undecimpunctata howardi* Barber | Cucurbitaceae cultivars | Central & S. USA |
| *D. undecimpunctata undecimpunctata* Mannerheim | Cucurbitaceae cultivars | W. USA |
| Acalymma | | |
| *A. bivittatum* (Fabricius) | Cucurbitaceae | Cuba, French Guiana, Brazil |
| *A. bivittulum amazonum* Bechyné | *Cucurbita maxima* Duchesne | Guiana, French Guiana, Brazil |
| *A. b. bivittulum* (Kirsch) | *C. maxima* | Argentina, Brazil, Bolivia, Peru |
| *A. b. exiguum* Bechyné & Bechyné | *C. maxima* | Ecuador, Peru |
| *A. blandulum* (Leconte) | *C. foetidissima* | Central & S.W. USA |
| *A. coruscum* (Harold) | *C. pepo, C. maxima* | Columbia, Venezuela |
| *A. gouldi* Barber | *Echinocystis lobata* (Michaux) Torrey & Gray, *Sicyos angulatus* Linnaeus | Central USA |
| *A. isogenum* Bechyné & Bechyné | *Cucurbita maxima* | Venezuela |
| *A. peregrinum* (Jacoby) | *Cucumis melo, Marah* | S. Texas, Mexico |
| *A. punctatum punctatum* Bechyné | *Cucurbita maxima* | Brazil |
| *A. p. coremum* Bechyné | *C. maxima* | Venezuela |
| *A. trivittatum* (Mannerheim) | Cucurbitaceae cultivars | W. USA, Costa Rica |
| *A. vinctum* (Leconte) | *Cucurbita okeechobeensis* (Small) Bailey | Florida, Georgia |
| *A. vittatum* (Fabricius) | Cucurbitaceae cultivars | Central & E. USA |
| Paranapiacaba | | |
| *P. connexa* (Leconte) | Cucurbitaceae | S. Texas, Mexico |
| *P. tricincta* Say | Cucurbitaceae | S.W. USA |

[a] Bogawat & Pandey (1967), Maulik (1936), Metcalf (1979), Smith (1966), Takizawa (1978), and Wilcox (1972).

*D. cristata* (Harris), *D. u. undecimpunctata*, *D. u. howardi*, *D. v. virgifera*, *Acalymma trivittatum*, *A. vittatum*, and *Aulacophora foveicollis* have been shown to feed compulsively upon pure crystalline cucurbitacins on inert surfaces, such as filter paper or silica gel (Chambliss & Jones 1966a; Sinha & Krishna 1969, 1970; Sharma & Hall 1971; Metcalf et al. 1980). Adults of *Diabrotica u. howardi* and *D. v. virgifera* have been shown to consume >2,000 mg/kg of Cuc B without any perceptible ill effects (Metcalf et al. 1980). Studies with $^{14}$C-labeled Cuc B fed to *D. balteata*, *D. barberi*, *D. cristata*, *D. u. howardi*, and *D. v. virgifera* demonstrated that these beetles possess well developed detoxication and excretory systems for Cucs (Ferguson & Fischer 1985).

These species of Diabroticina are able to detect nanogram quantities of Cucs by means of well-developed chemosensory organs located on the maxillary palpi (Metcalf et al. 1980), and the limit of response to pure cucurbitacins on silica gel thin layer plates varies with the individual species and the chemical nature of the Cuc (Table 4). The high degree of sensitivity and specificity of response of the beetles are demonstrated by the "beetle prints" resulting from the feeding of Diabroticina on Cucs extracted from Cucurbitaceae and separated by thin-layer chromatography (TLC) (Fig. 4). Using this technique, we have studied the

Table 4. — Limit of response (LR) of Diabroticina beetles to pure cucurbitacins.

| Species | LR in Micrograms of Cucurbitacin | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | B | D | E | F | G | I | L | Egly. |
| *Diabrotica balteata* | 0.01 | | | 10 | 3 | 5 | | 0.1 |
| *Diabrotica cristata* | 0.1 | | 0.3 | | | | | |
| *Diabrotica barberi* | 0.1 | | 0.3 | | | | | |
| *Diabrotica undecimpunctata howardi* | 0.001 | 0.03 | 0.01 | 1.0 | 3.0 | 0.1 | 0.01 | 0.05 |
| *Diabrotica undecimpunctata undecimpunctata* | 0.003 | | 0.03 | | | | | |
| *Diabrotica virgifera* | 0.01 | 0.1 | 0.3 | 0.1 | 3.0 | 0.3 | 1.0 | 0.03 |
| *Acalymma vittatum* | 0.3 | | 10 | | | | | 50 |

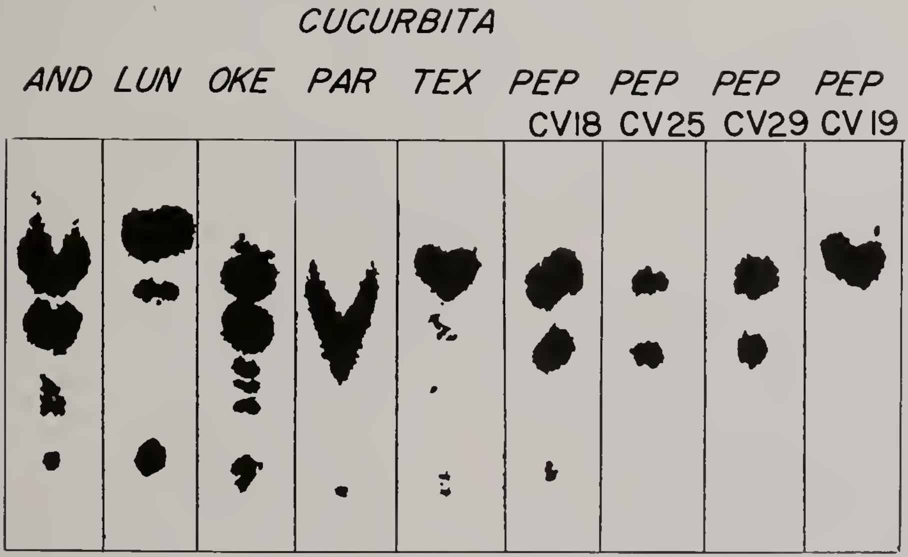

Fig. 4. – Beetle prints from feeding of *Diabrotica u. howardi* on thin-layer chromatograms of chloroform extracts of *Cucurbita* cotyledons. The dark areas eaten from the plates are the various cucurbitacins present. AND = *andreana*, LUN = *lundelliana*, OKE = *okeechobeensis*, PAR = *palmeri*, TEX = *texana*, and PEP = *pepo* cultivars. (Ferguson et al. 1983c. Reprinted with permission of the Journal Economic Entomology).

quantitative distribution of the Cucs in 18 species of *Cucurbita*, as shown in Table 5 (Metcalf et al. 1982). No Cucs were detectable in leaves, fruits, or roots of the domesticated species *C. ficifolia, C. maxima, C. mixta, C. moschata,* and *C. pepo* (zucchini) down to a limit of 0.02 mg per g of fresh weight. Indeed, fruits of these species would be inedible if Cucs were present. The Cucs content of the fruits of wild species ranged from 0.53 mg per g in *C. pedatifolia* to 3.2 mg per g in *C. andreana.* The nature of the Cucs present and the beetle feeding responses observed agree reasonably well with evolutionary groupings based on numerical taxonomy (Rhodes et al. 1968), cross compatibilities (Bemis et al. 1970), and isozyme analysis (Puchalski & Robinson 1978). Group (1) included the Cuc B- and Cuc D- forming species found in subgroup (a) *C. andreana* and *C. ecuadorensis* and subgroup (b) *C. gracilior, C. palmeri,* and *C. sororia.* Group (2) included the Cuc E- and I-forming species found in subgroup (a) *C. martinezii* and *C. okeechobeensis* and subgroup (b) *C. cylindrata. C. palmata, C. foetidissima,* and *C. texana* formed a preponderance of Cuc E glycoside (Metcalf et al. 1980, 1982).

The role of the Cucs as feeding stimulants was demonstrated conclusively by painting microgram quantities of Cuc B on soybean leaves, not eaten normally by *Diabrotica barberi, D. u. howardi,* and *D. v. virgifera.* All three species fed heavily upon leaf areas treated with Cuc B. In field experiments, these beetles ate a variety of weeds treated with Cuc extracts and homogenates of bitter *Cucurbita.* The plant *Iberis umbellata* Linnaeus, or candy tuft, (Cruciferae) is one of the few species outside the Cucurbitaceae known to produce Cucs. Plants of this species interspersed with bitter *Cucurbita* were massively attacked by *D. u. howardi* and *D. v. virgifera* and were completely defoliated and killed within 2 weeks. Thin-layer chromatography of *Iberis extracts isolated Cucs E and I.* which were readily fed upon by *Diabrotica* beetles (Metcalf et al. 1980).

Evaluation of Diabroticina feeding patterns on TLC chromatograms from extracts of *Cucurbita andreana* contain-

Table 5. — Cucurbitacin content of fruits of *Cucurbita* spp. [a]

| *Cucurbita* spp. | Cucurbitacin (mg per g of fresh weight) | | | | | |
|---|---|---|---|---|---|---|
| | B | D | E | I | Unknown | Glycoside |
| *andreana* Naudin | 2.78 | 0.42 | | | | |
| *cylindrata* Bailey | | | 0.10 | 0.18 | trace | 0.30 |
| *ecuadorensis* Cutler & Whitaker | 0.43 | 0.18 | | | | |
| *ficifolia* Bouché | | | - <0.02 - | | | |
| *foetidissima* Humboldt, Bonpland & Kunth | | | 0.36 | 1.59 | 0.49 | 0.91 |
| *gracilior* Bailey | 1.13 | 0.03 | | | | |
| *lundelliana* Bailey | 0.63 | 0.15 | | | trace | |
| *martinezii* Bailey | | | 0.36 | 0.45 | 0.03 | |
| *maxima* Duchesne | | | - <0.02 - | | | |
| *mixta* Pangalo | | | - <0.02 - | | | |
| *moschata* (Duchesne) Poiret | | | - <0.02 - | | | |
| *okecchobeensis* (Small) Bailey | | | 0.26 | 0.37 | 0.09 | |
| *palmata* S. Watson | | | | | | 0.83 |
| *palmeri* Bailey | 0.81 | 0.11 | | | 0.27 | |
| *pedatifolia* Bailey | 0.29 | 0.27 | | | | |
| *pepo* Linnaeus | | | - <0.02 - | | | |
| *saroia* Bailey | 0.54 | 0.27 | | | | |
| *texana* Gray | | | 0.07 | 0.37 | | 0.75 |

[a] Metcalf et al. (1982).

ing CuCucs B and D, *C. okeechobeensis* containing Cucs E and I, and *C. texana* containing Cuc E glycoside showed an almost identical qualitative response for *Diabrotica balteata, D. cristata, D. barberi, D. u. howardi, D. v. virgifera,* and *Acalymma vittatum* (Metcalf et al. 1980).

There is substantial evidence of the lengthy coevolutionary association of Cucurbitaceae plants and Luperini beetles. The genus *Cucurbita* is indigenous to the Americas, where it has existed since pre-Columbian times. It is considered to have its center of origin in the tropical or semitropical region of southern Mexico, from which the 27 species (22 wild, 5 cultivated) have radiated to North and South America (Whitaker & Bemis 1964, 1975). The present distribution of species of *Cucurbita* is (Whitaker & Bemis 1964): Southern Mexico and Central America, 14 species; Northern Mexico, 6 species; Northern South America, 4 species; Southern North America, 8 species.

The *Diabrotica* beetles have remarkably similar geographic distribution, as shown in Fig. 5. The putative area of origin of this genus is in northern South America or Central America, from which a few species have radiated into both southern South America and North America (data from Wilcox 1972).

Fig. 5 also shows the species distribution of the *Aulacophora* (Maulik 1936), the Old-World counterparts of the *Diabrotica,* which also must have coevolved with Cucurbitaceae. This genus appears to have evolved in Indonesia and to have radiated into southeast Asia, extending north to China and Siberia and south to Australia. The very close systematic relationships of the Aulacophorina and Diabroticina, the intimate association of both subtribes with Cucurbitaceae, and their common response to cucurbitacins strongly suggest a common ancestral co-evolution with an early cucurbitaceous species during a geologic per-

Fig. 5. – Distribution and numbers of described species of Diabroticina in the New World and Aulacophorina in the Old World. (Data from Wilcox 1972).

iod when continental land bridges were present (Metcalf 1979).

## KAIROMONE RECEPTOR INTERACTIONS IN THE DIABROTICINA

Among the Diabroticina beetles the primary sensory receptor organs that trigger the compulsive feeding response to the cucurbitacins are located on the maxillary palpi of both sexes. Surgical amputation of the maxillary palpi abolishes the compulsive feeding response, but this response is not altered by antennectomy (Metcalf et al. 1980). Scanning electronmicroscopy of these organs in *Diabrotica balteata, D. cristata, D. barberi, D. u. howardi, D. v. virgifera,* and *Acalymma vittatum* has demonstrated similar morphology of the sensory receptors in all species, and their ultra structure is under study (J. R. Larsen, University of Illinois, unpublished research). These species of Diabroticina respond qualitatively to the spectrum of Cucs found in choloroform extracts of *Cucurbita andreana, C. okeechobeensis,* and *C. texana*, as separated by TLC on silica gel thin layer plates, in an almost identical pattern (see Fig. 4). Thus, there is no evidence of any significant change in the spectrum of response to the Cucs by the various species of Diabroticina over an evolutionary period of more than 40 million years, as estimated from isozyme studies (Harvey et al. 1983). This evolutionary stability of receptor response is remarkable in view of the substantial differences in the present host preferences of these species of Diabroticina. The adults of a number of North American species have a proclivity for feeding on cucurbits and have been given trivial names suggesting this: *Diabrotica balteata,* the belted or banded cucumber beetle; *D. u. howardi,* the spotted cucumber beetle; *D. u. undecimpunctata* Mannerheim, the western spotted cucumber beetle; *D. picticornis* Horn, the painted cucumber beetle; *D. (Paranapiacaba) connexa* (LeConte), the saddled cucumber beetle; *Acalymma trivittatum,* the western striped cucumber beetle, and *Acalymma vittatum*, the striped cucumber beetle (Chittenden 1910). The most generalized feeders are probably *D. balteata,* whose adults also feed on cucumber, squash, melons, beans, soybeans, eggplant, and vetch, and *D. u. howardi* and *D. u. undecimpunctata,* whose adults feed on cucumbers, melons, squash, beans, soybeans, peas, cabbage, peppers, and corn (Chittenden 1910). *Acalymma trivittatum* and *A. vittatum* are more specialized, and the adults generally restrict their attacks to cucumber, squash, and melons. The northern corn rootworms, *Diabrotica barberi* Smith and Lawrence, and the western corn rootworm, *D. v. virgifera,* were originally described from adults collected on blossoms of *Cucurbita foetidissima* (Smith & Lawrence 1967) and *D. v. virgifera* adults readily attack cucumber, squash, and melons (Howe et al. 1976). The larvae of both species apparently develop only in the roots of grasses, especially corn, and the adults feed avidly on corn silks and pollen. Branson & Krysan (1981) suggest that both the northern and western corn rootworms have become pests of corn only relatively recently through convergent evolution. *D. cristata* is found almost exclusively in relict prairies and may develop only on the roots of prairie grasses, such as *Andropogon,* but the adults have been collected from squash blossoms (personal observation). The demonstration that functional Cuc receptors are present in these species suggests not only that they originally coevolved with the Cucurbitaceae, but also that the development of other host preferences may have been relatively recent (Branson & Krysan 1981).

The data in Table 4 indicating the limits of response (LR) for the various species of Diabroticina exposed to a variety of pure Cucs indicate that Cuc B was consistently detected at lower levels than was any of the other Cucs.

Therefore, it appears that Cuc B has maximum complementarity to the Cuc receptors on the maxillary palps and is likely to be the primitive Cuc to which the sensory receptor of an ancestral Luperini must have become evolutionarily tuned (Metcalf et al. 1980, 1982). This possibility is supported by the chemical resemblance of Cuc B to bryogenin, considered the parent tetracyclic triterpenoid formed from mevalonic acid (Geissman & Crout 1969). Bryogenin and Cuc B both have the cyclohexane moiety in ring A, differing from Cuc E, which has a partially aromatized ring with a C=C bond (Fig. 3). Cuc B is the dominant form found in the Cucurbitaceae and was detected in 91 percent of 46 species examined by Rehm et al. (1957); Cuc E was detected in 42 percent of the species. Furthermore, Cuc B was the dominant form found in the cotyledons of 19 species of wild *Cucurbita, Cucumis,* and *Citrullus* and in 46 commercial cultivars of these genera, even when the mature leaves and fruits contained Cuc E (Ferguson et al. 1983c). Cuc E is formed from Cuc B by an enzyme, cucurbitacin $\triangle^1$ dehydrogenase; Cuc D is formed from Cuc B and Cuc I from Cuc E by cucurbitacin acetyl esterase. The chemical relationships between these and other Cucs having alterations in the degree of oxygenation of ring A or in the unsaturation of the C23=C24 side chain are shown in Fig. 3. It appears that all of the common Cucs can be formed from Cuc B.

The sensitivity of response of the Diabroticina examined to the various pure Cucs (Table 4) was *D. u. howardi = D. u. undecimpunctata > D. balteata > D virgifera > D. barberi > D. cristata. Acalymma vittatum* is considerably less responsive. Cuc B was consistently detected at levels 0.1 – 0.3 of that of Cuc E, and the deacetoxy Cucs D and I were substantially less effective in triggering the compulsive feeding response than were Cucs B and E.

The changes in maxillary receptor sensitivity to the various Cucs demonstrated by all the species of Diabroticina examined impel speculation about the nature of the Cuc receptor. It seems likely that receptor depolarization follows allosteric changes in the receptor protein resulting from interactions of the free paired electrons associated with the several oxygen atoms in the Cuc molecules (Metcalf et al. 1980). The structural change in Cuc B by introduction of a single double bond at ring A to form Cuc E seems trivial (Fig. 3), yet this change produces a tenfold decrease in receptor affinity (Table 4). The introduction of the C=C into ring A substantially changes the orientation of the three contiguous O atoms (C3=O, C2-OH, and C11=O) from a staggered configuration in the cyclohexyl moiety of Cuc B to a planar configuration in Cuc E. This change seems ample, from my observations of molecular models, to decrease receptor affinity and depolarization (Metcalf et al. 1980). Cucs D and I exhibit about a tenfold decrease in receptor affinity compared with their C25 acetoxy derivatives, Cucs B and E (Fig. 3). This fact suggests that the acetoxy-C=O must also be involved in complete binding to the receptor.

## PLANT KAIROMONES AS ATTRACTANTS AND ARRESTANTS FOR INSECT PEST CONTROL

The intrinsic nature of the coevolutionary process that produced the specific interactions between plant kairomones and insect sensory organs that lead to profound behavioral changes suggests that kairomones can be employed for insect control in a variety of baits and traps. This use of the instinctual behavior of the insect pest in the presence of the kairomone chemical is analogous to the use of insect sex pheromones for population monitoring, removal trapping, and mating confusion (Shorey & McKelvey 1977; Mitchell 1981; Nordlund et al. 1981).

There has been surprisingly little application of this use of kairomones for insect control, and several of the most successful examples were developed without appreciation of the role of the kairomones in the chemical ecology of the pests (Mitchell 1981).

## Kairomone Baits for Monitoring and Controlling Dacini Fruitflies

Howlett (1915) first demonstrated that methyl eugenol was a specific attractant to males of several species of Dacini, including the oriental fruitfly *Dacus dorsalis*. During the outbreak of *D. dorsalis* in Hawaii following its discovery there in May 1946, oil of citronella was evaluated by the USDA as an attractant and was so effective that it was used as the standard substance for monitoring oriental fruitfly populations (Steiner 1952). Oil of citronella contains about 8 percent methyl eugenol, and it was soon demonstrated that the purified chemical was far superior in attracting male *D. dorsalis,* for which it is also an arrestant and compulsive feeding stimulant (Steiner 1952). Methyl eugenol was shown to attract male *D. dorsalis* upwind from as far as 0.5 mile away and to stimulate male fruitflies to compulsive feeding that can kill them from overindulgence. The use of methyl eugenol for population monitoring of *D. dorsalis* was rapidly adapted to a variety of invaginated glass and plastic traps containing water to drown the flies. Traps containing about 1 g of methyl eugenol trapped as many as 2,600 – 7,300 male *D. dorsalis* in a single day. The simple 8-oz (230-ml) bottle trap baited with methyl eugenol on a cotton wick has become a standard monitoring device to detect incipient oriental fruitfly invasions (Steiner 1957).

A simple box trap for area-wide control of *D. dorsalis* was developed by treating the inside of 3- × 12- × 16-inch (75- × 300- × 400-mm) wick boxes with 0.5 g of parathion insecticide as a wettable powder and overspraying with 2 ml of methyl eugenol (Steiner 1952). Such traps, open on one side, attracted and killed 13,000 – 15,000 fruitflies per trap. These traps were used to control *D. dorsalis* through male annihilation in pineapple fields in Hawaii, and it was shown that marked flies were attracted from as far as 1 – 1.5 miles (1.6 – 2.4 km) away. In a 125-acre (50-ha) pineapple field, 45 box traps killed thousands of male flies and substantially reduced the male fly population over an area of at least 4 square miles (10.4 km$^2$).

The male annihilation method has been refined by employing cane fiber blocks 2.5 inches (62.5 mm) square and 0.37 inch (9.25 mm) thick saturated with a bait mixture of 97 percent methyl eugenol and 3 percent naled insecticide (dimethyl 1,2-dibromo-2,2- dichloroethyl phosphate), so that each block contained about 23.3 g of methyl eugenol and 0.7 g of insecticide. These were dropped from aircraft at the rate of 125 per square mile (2.6 km$^2$) over the island of Rota in the Mariannas at about 2-week intervals for 8 months. The wild *D. dorsalis* population was monitored by methyl eugenol trapping and declined from a pretreatment count of 262 male *D. dorsalis* per trap to 18.4 males per trap after the first treatment and to 0.028 male per trap after the fourth treatment. No flies were caught after the 7th month, and the oriental fruitfly population was reduced by at least 99.6 percent (Steiner et al. 1965). This extremely efficient control effort used only 3.5 g of insecticide per acre (0.4 ha) per application and remains a classic demonstration of the efficiency and effectiveness of kairomone lures for insect pest control.

Raspberry ketone (Willison's lure) and its *p*-acetoxy-derivative, cue-lure, have been widely used for monitoring populations of male Dacini, such as the Queensland fruitfly, *Dacus tyroni*, and the melon fly, *D. cucurbitae*, that respond to this kairomone (Drew 1974; Drew & Hooper 1981). Fiberboard blocks 2.5 inches (62.5 mm) square and 0.5 inch (12.5 mm) thick were treated with a bait mixture of 95 percent cue-lure and 5 percent naled insecticide so that each block contained about 23.75 g of cue-lure and 1.25 g of insecticide. These blocks were tied 2–5 feet (0.6–1.5 m) above the ground on trees or stakes at the rate of about 585 blocks per square mile (2.6 $km^2$) over an isolated area of the island of Hawaii and were replaced with freshly treated blocks each month for 4 months (Cunningham & Steiner 1972). The wild *D. cucurbitae* population was monitored by cue-lure trapping and declined from a pretreatment count of 169 male *D. cucurbitae* per trap to 62 males per trap after the first treatment (96.3 percent decline) to 0.22 per trap after the fourth treatment (99.9 percent decline). This level of population reduction was maintained for over 60 days. This extremely efficient control effort used only 1.2 g of insecticide per acre (0.4 ha) per treatment and illustrates again the very high efficiency of kairomone baiting and the safety and specificity of this method of insect pest control.

The male annihilation technique using poisoned kairomone baits has produced high levels of control of several species of Dacini and, when applied to island populations, has resulted in the eradication of the Queensland fruitfly, *D. tyroni*, from Easter Island (Bateman et al. 1973). This method should be used with great caution against indigenous infestations because, as Hardy (1979) has emphasized, only a fraction of the 1,000 species of *Dacus* and related genera of Tephritidae are of commercial importance as pests infesting agricultural crops. Overenthusiastic efforts to eradicate pest species by the use of kairomone lures can lead to the devastation and even extinction of the endemic fauna in the Oriental, Australian, and Ethiopian zoogeographic regions. Thus no eradication program should be undertaken until the probable environmental impacts have been fully assessed.

## Kairomone Baits for Monitoring and Controlling Diabroticina Beetles

The tetracyclic triterpenoid cucurbitacins B and E are of high molecular weights and of very low volatility in contrast to methyl eugenol or raspberry ketone (the estimated v.p. of methyl eugenol is 0.01 mm Hg at 25 °C) and do not have any long-range vapor attractancy for Diabroticina beetles. The Cucs, however, resemble methyl eugenol and raspberry ketone in that they are powerful arrestants and compulsive feeding stimulants, detectable by Diabroticina beetles on inert surfaces at concentrations as low as 1 ng (Metcalf et al. 1980). In contrast to the phenylpropanoid kairomones for the Dacini, Cucs kairomones appear to be effective with both male and female Diabroticina.

Despite their lack of vapor attractancy, the Cucs can be used successfully to monitor Diabroticina beetle populations for integrated pest management (IPM) programs, and their kairomonal activity can be exploited for use in poison baits in a way that is analogous to the successful use of methyl eugenol and raspberry ketone for control of the Dacini. Whereas methyl eugenol and raspberry ketone and its analogue cue-lure are relatively simple organic chemicals that can be made synthetically, the Cucs are very complex chemicals that have not been synthesized. Nevertheless, the relatively high Cuc content of wild bitter *Cucurbita* provides a useful source of kairomones for study. Early experiment with Diabroticina beetles exposed equally to sliced bitter and sweet *Cucurbita* fruit demonstrated conclusively that the great preponderance of the Diabroticina beetles (95–98 percent) remained feeding on bitter fruits, such as *C. andreana* (Contardi 1939), *C. foetidissima* (Sharma & Hall 1973), and *C. pepo* (Howe et al. 1976). In a comparison of the arrestant powers of fresh, sliced fruits of 11 species of *Cucurbita* with total Cuc contents ranging from <0.02 mg per g (*C. max-*

ima, C. mixta, C. moschata, and *C. pepo*) to 3.20 mg per g (*C. andreana*), the correlation coefficient between average numbers of beetles feeding and Cuc content was 0.70 for *Diabrotica u. howardi* and 0.58 for *D. v. virgifera* (Metcalf et al. 1982). These bitter *Cucurbita* baits are rapidly consumed by Diabroticina beetle feeding, and the arrestant effect is lost within a day or two. The effectiveness can be prolonged for several weeks by sprinkling sliced bitter *Cucurbita* fruit with about 0.1 g of rapidly acting contact insecticide, such as trichlorfon or methomyl. Such treated bitter *Cucurbita* fruits remained effective in killing Diabroticina beetles for 3 weeks, even after heavy rains, and single fruit halves killed in excess of 2,000 beetles (Fig. 6) (Rhodes et al. 1980).

The prolonged arrestant power of dried bitter *Cucurbita* fruit for Diabroticina beetles is remarkable and illustrates the profound effect of the Cuc kairomones on beetle behavior. Ground or pelleted bitter Cuc fruits from *C. andreana* and *C. texana* or roots of *C. foetidissima* retain arrestant power for more than 3 years of storage indoors, and when impregnated with 0.1 percent w/w of a variety of carbamate and organophosphorus insecticides, are effective in arresting and killing Diabroticina beetles for 3 weeks or more under summer field conditions (Metcalf et al. 1983). These dry poisoned kairomone baits are being used to monitor Diabroticina populations to determine economic thresholds for IPM programs. Shaw et al. (1984) developed a 4-oz (120-ml) plastic vial, with holes to admit Diabroticina, baited with about 0.1 g of dried bitter *Cucurbita* bait containing carbaryl insecticide that is efficient and effective.

To use the Cuc kairomones for control of Diabroticina beetles, it is necessary to have an abundant source of bitter *Cucurbita* fruit, and wild *Cucurbita* spp. do not provide dependable sources of Cucs. They are more difficult to grow in temperate regions and yield less than domesticated species, and in some cases fruiting is dependent upon the photo-period. Genes conrolling the formation of Cucs were transferred to domesticated cultivars by crossing *C. andreana* × *C. maxima* to produce long-vined plants with large fruits, averaging 3.90 kg and containing a total of 1.26 mg of Cuc B and D per gram of fresh weight. The dried bait contained 5.0 mg of Cucs per gram. A hybrid of *C. texana* × *C. pepo* produced bushy plants with fruits averaging 0.73 kg and containing a total of 0.48 mg of Cucs E, I, and E-glycoside per gram of fresh weight. The dried bait contained 6.1 mg of Cucs ($F_1$ fruit) and 3.0 mg of Cucs ($F_2$ fruit) per gram (Rhodes et al. 1980; Metcalf et al. 1983). Another source of Cuc kairomones is in the roots of *C. foetidissima*, which contain about 3.1 mg of Cucs E, I, and E-glycoside per gram of fresh weight (Metcalf et al. 1982). Dried *C. foetidissima* roots, grown as a semicommercial crop for starch production in Arizona, contained 4.0 mg of Cucs per gram (Berry et al. 1978).

These air-dried and ground *Cucurbit* baits were impregnated with a variety of insecticides, including the carbamates, carbaryl, carbofuran, bendicarb, and methomyl; the organophosphates, malathion, dimethoate, terbufos, and isofenphos; and the pyrethroids, fenvalerate, permethrin, and decamethrin. It was determined that the most effective concentrations of insecticides were 0.1 percent w/w for carbamates and organophosphates and 0.01 percent w/w for pyrethroids. Such baits have been evaluated for Diabroticina beetle control in cucurbits, sweet corn, and dent corn by broadcasting them at rates of 10–100 lb (4.5–45 kg) of bait per acre (0.4 ha). Applications of these baits at 10–30 lb (4.5–13.5 kg) per acre produced reductions of adult *Diabrotica u. howardi*, *D. virgifera*, and *Acalymma vittatum* ranging from 75 to 99+ percent within 1 to 3 days. Baits poisoned with methomyl and isofenphos were effective at application rates of 4.5–13.5 g of insecticide per acre (0.4 ha), and the decamethrin bait at rates as low as 0.45 g per acre

Fig. 6.–*Diabrotica* beetles killed after 5 days of feeding on cut fruit of *C. pepo* × *C. texana* hybrid dusted with 0.1 g of methomyl insecticide (Rhodes et al. 1980).

(0.4 ha). (Metcalf et al. 1982, 1983a). In experiments in sweet and dent corn such applications killed from 160,000 to 230,000 Diabroticina beetles per acre (0.4 ha) and remained effective for at least 2 weeks. A notable feature of the Cuc-kairomone insecticide baits is that the quantity of insecticide required per unit of area is only about 1 percent of that required for conventional spray applications for Diabroticina beetle control. The applications are highly selective because of the kairomonal effect on the Diabroticina, and other insects, including beneficial insects, are not appreciably affected.

## HOST-PLANT RESISTANCE BY ANTIXENOSIS (NONPREFERENCE)

Antixenosis is a major type of host-plant resistance to insect attack in which the plant lacks the characteristics desired by insect pests and is an unsuitable host. Antixenosis, therefore, is the major resistance factor limiting most phytophagous insects to a monophagous or oligophagous host range. Increasing appreciation of the role of plant allelochemics acting as kairomones, suggests that genetic manipulations to remove them from cultivars is a logical approach to host-plant resistance. Indeed, this removal has occurred inadvertently in the Cucurbitaceae from primitive man's efforts to find palatable squash, melons, and cucumbers free of the bitter cucurbitacins. However, antixenosis has had only limited exploitation in the development of pest-resistant cultivars compared with the development of antibiosis, involving genetic manipulation to produce or increase allelochemics or other factors adverse to host selection and pest development and reproduction (Kogan 1983).

The importance of antixenosis as a mechanism for host-plant resistance in the Cucurbitaceae to cucumber beetles (Diabroticina) has been demonstrated for the squash *Cucurbita pepo* (Nath & Hall 1965), the watermelon *Citrullus lanatus* (Chambliss & Jones 1966b), and the cucumber *Cucumis sativus* (DaCosta & Jones 1971b). In the Cucurbitaceae, cucurbitacin synthesis is initiated by a single dominant "bitter gene," *Bi*, and antixenotic resistance is associated with the recessive phenotype, *bi bi* (DaCosta & Jones 1971a; Robinson et al. 1976). Nonbitter fruit may develop from bitter seedlings in the presence of a modifier suppressing synthesis in the fruit. Quantitative estimations of the total Cuc content in *Cucurbita* have shown a partial dominance for low Cuc content with a multigenic additive type of inheritance (Nath & Hall 1965). The Cuc content of the cotyledon leaves appears to be substantially independent of that in mature leaves and fruits (Ferguson et al. 1983b).

Protection of the early growth stages of Cucurbitaceae cultivars from attack by Diabroticina beetles is a major necessity for the successful survival of these plants. Study of 46 cultivars of *Cucurbita, Cucumis,* and *Citrullus* showed that substantial amounts of Cucs were present in the seedling stages of 29 of these cultivars at a limit of detection of about 0.1 ppm of fresh weight. These Cucs were demonstrated by extraction and thin-layer chromatography, followed by the feeding of the spotted cucumber beetle, *Diabrotica u. howardi*, and the banded cucumber beetle, *D. balteata* (Ferguson et al. 1983b).

Field experiments showed that there was almost complete correlation between Cuc content of the cotyledon leaves of 25 *Cucurbita* cultivars and the extent of the destruction of seedling plants by early spring and summer feeding of *Diabrotica u. howardi* and *Acalymma vittatum* beetles (Ferguson et al. 1983b). This demonstration of the value of antixenosis provides a useful example of means for the selection of *Cucurbita* cultivars with substantial antixenotic host-plant resistance to Diabroticina pests. Such antixenotic host-plant resistant varieties can play an important role in IPM programs. It should be emphasized that the cucurbitacins also function as allomones to confer host-plant protection against a variety of herbivores apart from the Diabroticina. Therefore, the ultimate effect of antixenosis in crop protection is one of balance. For the Cucurbitaceae, the depradations of the Diabroticina and the wilt diseases that they innoculate are so severe that the balance appears to be tilted strongly in favor of antixenotic protection.

## KAIROMONES IN TRAP CROPS

From evolutionary considerations, it appears that the use of kairomones *in situ* in plants attractive to insects should provide an optimum way to control insects (Martin 1940:317). The principle of insect control by "trap cropping" has its origin in folklore but can be developed on a rational basis through knowledge of the qualitative and quantitative nature of the kairomone contents responsible for insect attraction, arrest, compulsive feeding, and oviposition. Curtis (1860) recommended controling the parsnip webworms, *Depressaria depressella* (Hübner) and *D. daucella* (Denis & Schiffermüller), (Oechophoridae) by setting parsnip plants (*Heracleum sphondylium* Linnaeus) 6–10 feet (1.8–3.0 m) apart among carrots (*Daucus carota* Linnaeus) (Umbelliferae). The webworm moths prefer to lay their eggs upon the parsnips, and the larvae develop in the parsnip heads and can be destroyed by cutting and burning or by drowning.

A modern example of successful trap cropping is Newsom's (1978) suggestion that lima beans (*Phaseolus lunatus* Linnaeus) planted contiguously with soybeans (*Glycine max* (L.) Merrill) will trap the Mexican bean beetle, *Epilachna varivestis* Mulsant. The principle of trap cropping is stated to be an important component of IPM for soybean pests, reflecting economy, minimum adverse effects on beneficial insects, reduction of environmental pollution by pesticides, and minimal selective pressure to delay insecticide resistance.

Detailed knowledge of the kairomones present in plant species and varieties now affords a firm scientific basis for the application of the trap-crop principle. Contardi (1939) speculated about the use of bitter *Cucurbita andreana* as a trap crop to protect cucurbit cultivars from attack by *Diabrotica speciosa*. A single vine of *Cucurbita ecuadorensis*, whose leaves contain a total of 0.41 mg of Cuc B per gram of fresh weight, planted at the periphery of a 0.1-acre (0.04-ha) melon patch of *Cucumis melo* cultivar was observed to have arrested hundreds of spotted cucumber beetles, while only a single beetle was found in the muskmelon. Experiments using a design of hybrid *Cucurbita andrena* × *C. maxima* plants, one on each side of plots of 20 muskmelon plants, *Cucumis melo*, showed that 82 percent of *Diabrotica u. howardi, D. v. virgifera*, and *Acalymma vittatum* were found on the trap crop (average 18 per plant) compared with those found on the melons (average 4.2 per plant) (unpublished data). Such trap crops can be used in conjunction with occasional applications of contact insecticides to destroy the pests on the trap crop, or the trap crop can be planted over an application of granular systemic insecticide. Scientifically designed trap cropping, employing species or cultivars with high kairomone levels that do not hybridize with cultivars, offers a technological challenge to the organic farmer and an economical method for substantially decreasing the use of insecticides.

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# Early Contributions of Insect Toxicology To the Evolution of Environmental Toxicology

Allan S. Felsot

The celebration of an anniversary connotes the remembrance of the past from the perspective of the present with anticipation for the future. Science, like law, is built upon precedent. The continued advancement of any scientific endeavor must entail a periodic assessment of where that discipline has been. Historical observations inevitably lead to a better understanding of the present state of the art and of future needs. It is appropriate on the occasion of the 125th anniversary of the Illinois Natural History Survey to examine the historical roots of one of its disciplines. The study of environmental toxicology is relatively new, but it has a long tradition of support within both the Survey's Section of Economic Entomology and the University of Illinois' Department of Entomology.

Environmental toxicology is a broadly based discipline that involves the integrated efforts of scientists from many other disciplines. It is currently enjoying unprecedented public attention in the media. Not since the publication of *Silent Spring* (Carson 1962) has more public attention been focused on environmental contamination from chemicals and the potential biological effects. Amidst all the controversy surrounding the manufacture, use, and disposal of synthetic organic chemicals, it is easy to forget how this environmental awareness came about. More importantly, the evolution of the science that provided the fundamental basis for this awareness has become obscured.

It is hypothesized that the field of environmental toxicology began as a subdiscipline of applied entomology. Early environmental toxicological research was mainly conducted by economic entomologists who needed to know the effective dose required to kill pest insects and the environmental factors that would affect the efficacy of the pest control operation. Today, the Entomological Society of America recognizes pesticide chemistry and toxicology as research areas within the scope of two of its disciplinary sections. The objective of this paper is to document the early contributions of economic entomologists (especially insect toxicologists) to the development of environmental toxicology by examining the entomological literature prior to 1962 (the year of publication of Carson's *Silent Spring*). This objective was accomplished by scanning the *Journal of Economic Entomology* (JEE), volume 1 (1908) through volume 55 (1962), for papers that dealt with environmental toxicology. In addition, papers from other journals were cited if they seemed to have had a significant influence on the content and direction of the insect toxicological research reported in JEE.

Seven areas of research that form the essence of modern environmental toxicology could be seen in the applied entomological literature. These included the measurement of toxicity; symptomology, mode of action, and metabolism; insecticide resistance; pesticide selectivity and comparative toxicology; insecticide residues and analytical methods development; hazard evaluation; and environmental chemodynamics. The contributions of entomologists to each of these areas were reviewed.

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## MEASUREMENT OF TOXICITY

Chemicals have long been used to help control insect pests. Early accounts of insect toxicology were anecdotal with little quantitative data from which to determine effective dosages even though the number of chemicals available was very limited by today's standards. Economic entomologists recognized the need to develop a standardized system for comparing the toxicity of different chemicals and for determining the efficacy of control.

Early studies were devoted to finding appropriate bioassays for the determination of toxicity of cyanide fumigants. Coleman (1911) developed a bioassay to determine the most effective concentration of cyanide gas against scale insects. He observed mortality of insects in the laboratory at one-sixteenth the dosage that had been prevalent in fumigation work. Hartzell (1924) was the first to use correlation analysis to study the relation of control efficiency to dosage, temperature, and percentage of open space. Dosage was found to exert the greatest influence on control. Abbott (1925) presented a technique that is still used routinely for correcting the observed mortality that may occur in the untreated population of a bioassay.

A technique for comparing the relative toxicities of several chemicals to a variety of invertebrate and vertebrate species was first reported by Marcovitch (1928). He adapted a mathematical formula, using time and concentration as variables, to determine the numerical toxicities of arsenical and fluorine compounds. He suggested that the mosquito be used as a standard test organism in insect toxicology as the white rat was for pharmacological studies. Comparative toxicity tests of different compounds were also studied by Campbell (1930). Campbell used the concept of median lethal dose, the dose which kills 50 percent of a large group of animals, to express the toxicity of different compounds to the silkworm and mosquito. The concept of median lethal dose had been proposed earlier by Trevan (1927) to replace the prevalent expression of minimal lethal dose, which was regarded as highly variable. Campbell further showed the importance of the route of exposure to the toxicity of a compound. Shepard & Richardson (1931) also used Trevan's (1927) ideas to draw "toxicity curves," described as being characteristic of a specific insecticide regardless of how the dosage was measured.

After Trevan's concept of median lethal dose was published, many toxicologists observed that the response of animal populations to increasing dosages of a toxicant followed a sigmoidal pattern. Bliss (1934) used this characteristic phenomenon to develop a standardized technique for determining mortality at a specified dosage. He transformed dosage to logarithmic units and percent mortality to probability units that he termed probits. The dosage-mortality curve became linear and thus amenable to regression analysis. In later work, Bliss (1935a) developed statistical procedures for calculating dosage-mortality curves. In a related paper Bliss (1935b) introduced the term "LD50" to replace median lethal dose in comparisons of dosage-mortality data. Later, Bliss developed techniques for expressing mortality relative to time of exposure and the relationship between exposure time and concentration (Bliss 1937, 1940). Although researchers have studied the intricacies of the dosage-mortality curve and have suggested improvements (e.g., Sun & Shepard 1947; Wadley & Sullivan 1943; Beard 1949; Lanchester 1951), Bliss' techniques have remained standard practice in all fields of toxicology.

## SYMTOMOLOGY, MODE OF ACTION AND METABOLISM

Observations on pesticide symptomology, mode of action, and metabolism are classified today as pharmacokinetic or toxicodynamic studies. Early observations of symptoms exhibited by poisoned insects gave clues to the mode of insecticide action (Shafer 1911a,b; Tischler 1935). Mode of action studies gradually became more sophisticated with the evolution and advancements in biochemistry. For example, Fink (1927) compared glutathione levels in normal insects and in insects treated with arsenicals. His observations were in agreement with the published findings on arsenic toxicity in vertebrates (Voegtlin et al. 1925), that arsenic interfered with the normal functioning of glutathione. Metcalf & March (1949) produced a highly cited study on the mode of action of parathion in insects that influenced the course of insect toxicology research. These authors conducted pioneer studies on the relation of the chemical structure of a series of organophosphorus insecticides to toxicity and cholinesterase inhibition. They were the first to show that there was a direct relationship between in vitro cholinesterase inhibition and in vivo toxicity.

The importance of metabolism in explaining differential toxicity among insect species was recognized early in the entomological literature (Fernald 1908). Prior to World War II few metabolism studies were reported because analytical methods were too insensitive for the determination of toxicants and metabolites in small tissue samples. However, the value of radiotracer methodology as a sensitive detection technique was shown in studies on arsenic disposition in the silkworm (Campbell & Lukens 1931; Norton & Hansberry 1941). After the introduction of DDT, the metabolism of chlorinated hydrocarbons in insects was studied by using only wet chemical methods of analysis (Ferguson & Kearns 1949; Sternburg et al. 1950; Sternburg & Kearns 1956). Most studies on insect metabolism after 1950 employed radioisotopes of the chlorinated hydrocarbon and organophosphorus insecticides (e.g., Roan et al. 1950; Lindquist et at. 1951a,b). In the 1950's and thereafter radioisotopes were increasingly used to study the metabolism and distribution of insecticides in nontarget vertebrates (e.g., Pankaskie et al. 1952; Robbins et al. 1956; March et al. 1956a,b; Lindquist et al. 1958; Kaplanis et al. 1959).

Another area of early toxicodynamic research in the entomological literature is the study of the effect of chemical interactions on toxicity and metabolism. Specifically, synergistic interactions between insecticides and nontoxic compounds, such as sesamin, were found to be important in increasing the toxicity of the unstable pyrethrums (Haller et al. 1942; Kerr 1951). Robbins et al. (1959) first reported the synergism of organophosphates by piperonyl butoxide in mammals. The interactions between synthetic organic insecticides and botanical insecticides were also studied (Sun 1948).

## INSECTICIDE RESISTANCE

The study of insecticide resistance has received a great deal of attention by insect toxicologists. Although many reviews of this subject have appeared since the 1940's (e.g., Quayle 1943; Babers 1953; Brown 1968; Georghiou & Taylor 1976), several points pertinent to the development of environmental toxicology should be noted. First, insect resistance was originally reported in 1914 by Melander and involved the decreased effectiveness of lime-sulphur against the San Jose scale. Prior to 1940 most reports involved resistance of scale insects or the codling moth to various fumigants (Quayle 1943). After the introduction and widespread use of DDT in the mid-1940's, reports of resistance grew exponentially. March & Metcalf (1949a,b) were probably the first in the United States to report both DDT resistance and possible cross resistance to other chlorinated hydrocarbon insecticides in houseflies. Until that time most resistance studies involved anecdotal reports of decreased control of pests in the field or the comparison of insecticide toxicity against laboratory strains and field-collected populations. A breakthrough in understanding the biochemical basis of resistance came with the reports of differences in DDT metabolism between susceptible and resistant houseflies (Sternburg et al. 1950; Perry & Hoskins 1951). When Sternburg et al. (1953) reported that DDT was enzymatically dehydrochlorinated by resistant houseflies, the stage was set for sophisticated studies on detoxication mechanisms and the biochemical genetics of resistance.

## PESTICIDE SELECTIVITY AND COMPARATIVE TOXICOLOGY

Pesticide selectivity refers to the determination of the relationship between chemical structure and toxicity in various target and nontarget species. Comparative toxicology includes studies of differences among invertebrates and vertebrates in detoxication mechanisms and pesticide interactions with biochemical targets.

Kearns and his coworkers (e.g., Kearns & Flint 1937; Metcalf & Kearns 1941; Dahm & Kearns 1941) pioneered the concept of testing a large number of compounds in a homologous series against different insects to determine the effect of chemical structure on toxicity. Early studies focused on nitrogen-containing synthetic organics, such as cyclohexylamine, picramic acid, toluenesulfonyl chloride, and alkyl secondary amines. Other structure-activity studies followed with investigations of phosphorous esters (Ludvik & Decker 1947, 1951), N-heterocyclics (King & Frear 1943), DDT analogs (Metcalf 1948), and N-methyl carbamates (Metcalf et al. 1960, 1962). Some studies were qualitative in the sense that long lists of compounds and percentages of mortality were presented. Other studies became more quantitative by graphing the relationship between mortality and specific chemical properties (e.g., Dahm & Kearns 1941; Fukuto et al. 1961; Metcalf et al. 1962).

Pesticide selectivity studies were important in reconciling the role of biological control of insect pests with that of chemical control. For example, Ripper et al. (1951) published a comprehensive study on the comparative toxicity of insecticides between pests and their natural enemies. Today, quantitative structure-activity correlations play an important role in the discovery of new pest control agents and in the development of compounds that are selective for target organisms.

Although research had been conducted on the toxic effects of pesticides on nontarget vertebrates, few studies directly compared responses of insects and vertebrates before the advent of the synthetic organic insecticides. Marcovitch (1928) was perhaps the first entomologist to compare the toxicity of inorganic insecticides between mosquitoes, earthworms, and rabbits. Goldfish and cockroaches were compared in an investigation of the toxic effects of nicotine (Ellisor 1936). The first comprehensive comparative toxicological study was reported by Metcalf & March (1950). These workers compared the properties of acetylcholinesterase from the bee, the housefly, and the mouse to study the relationship between parathion derivatives and insecticidal action. The motivation behind studies of this nature is clear from the authors' conclusion, "A detailed knowledge of the properties of various cholinesterases and correlation of the structure of various organic phosphate anticholinesterases with their specific action may result in the development of insecticides with a greater margin of safety to warm-blooded animals than those currently in use, and may enable the entomologist to select compounds toxic to certain insect pests, but relatively harmless to beneficial parasites and predators." Metcalf & March (1950) greatly influenced the course of toxicology as evidenced by the volume of research devoted to comparative toxicological studies in the 1950's and 1960's (e.g., Johnson et al. 1952; Casida & Stahmann 1953; March et al. 1955, 1956a; O'Brien 1956, 1957a,b; O'Brien et al. 1958; Krueger & Casida 1957; Krueger & O'Brien 1959; Krueger et al. 1960; Casida et al. 1960; Afsharpour & O'Brien 1962).

## INSECTICIDE RESIDUES AND DEVELOPMENT OF ANALYTICAL METHODS

The problem of pesticide residues on food and in the environment has concerned entomologists since the early 1900's. JEE has long served as a forum for the reporting of residues. This function was especially important when there was essentially no other outlet for this kind of investigation. Prior to World War II and the introduction of DDT, most investigations centered on the occurrence of arsenic and lead residues owing to the heavy spraying of lead arsenate for the control of orchard pests. Early studies were concerned with arsenic residues in soils because of the potential for phytotoxicity to trees in alkaline soils (Ball et al. 1910; Headden 1910). Later studies measured the arsenic and lead content of sprayed apples (O'Kane 1913; MacLeod et al. 1927; Hartzell & Wilcoxon 1927, 1928; McLean & Weber 1928). Attention was also given to residues of the organic insecticides, nicotine, and derris (Norton & Billings 1941; Cassil 1941).

The introduction of DDT into general use in agriculture greatly increased the amount of insecticides used. Consequently, the attention devoted to pesticide residues greatly increased. The prolonged persistence of DDT was quickly recognized. Almost every crop that had been sprayed with DDT was studied for residues (e.g., Wilson et al. 1946b; Borden 1947; Smith et al. 1948a; Eden & Arant 1948). Residues of other synthetic organic insecticides, especially the organophosphates, were investigated almost as soon as they were introduced (e.g., Ginsburg et al. 1949, 1950; Hoskins 1949; Smith et al. 1952; Gunther & Jeppson 1954; Gunther et al. 1954; Brett & Bowery 1958).

The tremendous interest in pesticide residues after the introduction of the synthetic organics was more than mere concern about the possibility of exceeding established tolerances. Shortly after the general introduction of DDT it was discovered that this chemical could be bioconcentrated in milk and passed through the food chain (Telford & Guthrie 1945; Woodward et al. 1945; Wilson et al. 1946a). Many reports on the occurrence of DDT and other chlorinated hydrocarbon insecticides in milk and meat products appeared in JEE after 1946 (e.g., Smith et al. 1948b; Carter et al. 1949a,b; Claborn et al. 1950a,b; Frear et al. 1950; Bushland et al. 1950; Fahey et al. 1955; Ely et al. 1957). These studies generally showed that DDT could bioconcentrate in milk regardless of whether the insecticide was applied directly to cows, barns, or feed. Studies of organophosphate and carbamate insecticide residues in milk soon followed the DDT studies, but these indicated no significant bioconcentration (Goulding & Terriere 1959; Eheart et al. 1962).

Pesticide residues were also studied in poultry and eggs. Lindane, a chlorinated hydrocarbon, was found at high levels in fat and eggs several months after poultry houses had been sprayed, and recommendations for its use were cancelled (Ivey et al. 1961). Residues of Co-Ral, an organophosphate, were extensively studied by Dorough et al. (1961a,b). These authors emphasized the need also to study metabolite residues. Bioconcentration of carbamate insecticides was shown to be insignificant in a study of carbaryl residues in poultry products (McCay & Arthur 1962).

It should be noted that residue studies of organophosphate and carbamate insecticides during the 1950's and 1960's were using detection limits of approximately 0.1 ppm. Today, detection limits easily reach the 0.01 or 0.001 ppm level, and the probability of finding "biodegradable" pesticide residues in food has increased accordingly.

Food processing, such as the milling of wheat, was found to aid in residue reduction (Schesser et al. 1958). Siakotos (1956b) observed that vaporized lindane could enter stored packaged foods regardless of the container. Since it was observed that pesticide residues on food were generally inevitable, some attention was devoted to techniques for residue removal. A number of studies were conducted on the removal of lead arsenate residues from fruit (Robinson 1929; Fisher 1931; Weber & McLean 1933); later, the effect of washing on organophosphates was studied (Smith et al. 1955).

Concomitant with the need for accurate pesticide residue determinations was the development of sensitive analytical methods. Although other journals published analytical methods for pesticide residues (e.g., *Journal of the Association of Agricultural Chemists,* published prior to World War II, and the *Journal of Agricultural and Food Chemistry,* initiated in 1953), JEE had been a reliable forum for this kind of information since its inception. Early reports included methods for the analysis of nicotine (Safro 1917), lead arsenate (Hamilton & Smith 1925; Ginsburg 1928), oil (Ebeling 1940; McCall & Kagy 1940), and rotenone (Gunther 1942).

The widespread use of the synthetic organic pesticides stimulated investigation of more sophisticated and diverse techniques that were required for the analysis of the growing number of sampling matrices (Carter 1955). Originally the chlorinated hydrocarbons were determined by total chlorine analysis (Ginsburg 1946). Eventually, chromatographic separation methods and, later, colorimetric analysis were adopted for the analysis of many organochlorine insecticides (e.g., DDT, Schechter & Haller 1945; aldrin and dieldrin, O'Donnell et al. 1954, 1955; heptachlor and chlordane, Polen & Silverman 1952; lindane, Schechter & Hornstein, 1952; EDB, Sinclair & Crandall 1952). Radiolabelled pesticides were useful for testing the extraction of residues from complex matrices, such as milk (Timmerman et al. 1961). A cholinesterase-inhibition technique, useful for detecting organophosphate insecticides (Giang & Hall 1951), was modified for analyzing weak inhibitors, such as the organophosphorodithioates (Miskus et al. 1959; Miskus & Hassan 1959). The bioassay of extracts, using mosquito larvae, was employed as a sensitive technique for the detection of toxic compounds and metabolites (Bushland 1951; Hartzell 1952). Sampling techniques to ensure reliable residue data were also studied (Cassil et al. 1943; Anderson & Gunther 1951; Van Middelem et al. 1956; Huddleston et al. 1960b; Lichtenstein et al. 1960).

In sum, the literature on insecticide residues shows a long-standing and deep concern among entomologists about health hazards in food supplies. Perhaps the prevailing philosophy was expressed best by White (1934), who stated at a meeting of the American Association of Economic Entomologists, "Let us not again go along for years putting on other poisons in total ignorance of the amounts going to the consumer and of the effects upon his health." This theme was acted upon in 1951 when the chairmen of most midwestern departments of entomology met in Chicago and prepared the outline of a research project entitled, "Hazards Resulting from the Use and Misuse of Pesticides and Means for their Elimination" (E.P. Lichtenstein personal communication). This project was activated in 1954 and represented one of the first regional projects (NC-19) established in entomology. The objective of this cooperative venture was to isolate, define, minimize, or eliminate hazards connected with the use of pesticides.

## HAZARD EVALUATION

Hazard evaluation involves the determination of acute and chronic effects on nontarget organisms and on the environment from direct or indirect exposure to pesticides or their metabolites. Four main areas of hazard evaluation research that have appeared in the entomological literature are hazards to livestock and other mammals; hazards to nontarget insects, fish, and birds; effects on soil biota and plants; and effects on human health.

The use of insecticides to protect livestock from insect infestations that might reduce production efficiency had been investigated since the late 1920's (Melvin 1932). Naturally, the safety of the animals was a major concern. Early studies focused on the physiological and toxic effects of oil sprays on cattle (Melvin 1932; Freeborn et al. 1934; Atkeson et al. 1944). No acute effects owing to the treatment of forage with pyrethrum (De Ong 1937) or cryolite (Wilford & Mott 1944) were observed in pastured livestock. In other tests it was observed that the injection of pyrethrum extract into rats produced severe adverse reactions (Leonard 1942), but a similar mode of exposure to cryolite failed to produce acute toxic symptoms (Sweetman & Bourne 1944). Feeding studies with chickens showed no adverse effects with low doses of arsenic bait, but it reduced egg laying at high doses (Wilson & Holmes 1936).

The first widespread use of DDT after World War II was for the control of livestock pests. Immediately after the introduction of DDT there was a proliferation of reports on its effects on a wide variety of animals. Much of this research attempted to etablish safe levels of insecticide exposure resulting from single or repeated adminstrations by direct spraying or by feeding (e.g., Orr & Mott 1945; Telford & Guthrie 1946; Wilson et al. 1946a; Bushland et al. 1948; Batte & Turk 1948; Welch 1948; Radeleff 1950). Both acute toxic symptoms and histopathological changes were recorded in response to extremely high dosages and dosages likely to be received under normal use conditions. In general, low dosages of many of the chlorinated hydrocarbons had little effect, but moderate to severe histopathological effects were noted at the highest dosages.

Ingle (1947) used white rats to compare the acute and chronic toxicities of chlordane and DDT. From 1950 to 1955 there were a number of studies on the toxicity of the new chlorinated cyclodiene insecticides to poultry (Eden 1951; Turner & Eden 1952; Arant 1952; Sherman & Rosenberg 1953, 1954). Moore (1952) studied the toxic effect of lindane vapors on canaries and pigeons.

After the early 1950's, research was directed to the acute effects of exposure to the organophosphate insecticides. Studies were conducted on the toxicity of direct application (Furman & Weinmann 1956), exposure through treated forage (Dobson et al. 1960), and exposure to vapors (Tracy et al. 1960). Research was also directed toward the toxicity of systemic organophosphate insecticides intentionally added to feeds (Radeleff & Woodard 1956, 1957). Methods for measuring cholinesterase activity in erythrocytes were developed to determine the degree of exposure of livestock to organophosphate residues (Robbins et al. 1958; Hermenze & Goodwin 1959). Effects of organochlorine and organophosphate insecticides on the metabolism and motility of mammalian spermatozoa were studied by Beck (1953).

The use of DDT and organophosphates as mosquito larvicides stimulated research on the acute toxicity of these pesticides to fish and aquatic invertebrates (Ginsburg 1945, 1947; Eide et al. 1945; Darsie & Corriden 1959; Mulla & Isaak 1961). Some studies determined the acute toxicity to fish of insecticides that could reach water through indirect routes (Schulze et al. 1952; Haynes et al. 1958). Other studies investigated the ecological effects of insecticides on aquatic communites (Tiller & Cory 1947; Hitchcock 1960; Webb 1960).

Arsenic baits used in grasshopper control were found nontoxic to pheasants (Lilly 1940). DDT-treated insects were fed to nestling birds in one study, and toxicity was only manifested when the birds' food supply was limited (George & Mitchell 1947).

Although the effects of insecticides on bees had received much attention before 1900 (Shaw 1941), little research had been conducted on the hazards of insecticides to other beneficial insects, including predators and parasites, before the introduction of DDT (Haug & Peterson 1938). Both arsenicals and DDT were the focus of much of the research on pollinators before 1950 (Doane 1923; Webster & Crews 1934; Linsley & MacSwain 1947). Observations by many workers of the resurgence of pest populations and the emergence of secondary pests after crops were sprayed with DDT (DeBach 1947; Newson & Smith 1949; Griffiths 1951) stimulated further research on the acute toxicity of various insecticides to beneficial insects (Ripper et al. 1951).

Concern for the potential hazards associated with pesticide accumulation in soil was manifested long before the introduction of the persistent chlorinated hydrocarbons. Hyslop (1914) expressed concern about the effect of cyanide on beneficial soil microbiota. Others studied the effect of the accumulation of lead and calcium arsenate on their phytoxicity (Scott & Karr 1942; Fleming et al. 1943). The concern with adverse effects on microbiota and with phytoxicity continued after the introduction of DDT (Wilson & Choudhri 1946; Morrison et al. 1948; Cullinan 1949; Stitt & Evanson 1949; Gould & Hamstead 1951; Simkover & Shenefelt 1951) even though the accumulation of DDT residues from earlier applications had not been recognized until the 1950's (Chisholm et al. 1950; Ginsburg & Reed 1954; Lichtenstein 1957). Most studies did show some phytotoxic effects from chlorinated hydrocarbons, such as lindane (Morrison et al. 1948). In general, few effects on soil microorganisms or microarthropods were observed after insecticide treatments (Bollen et al. 1954a,b; Hartenstein 1960).

Since the early 1970's great emphasis has been placed on the assessment of human exposure to pesticides. Recently a research conference and workshop on minimizing occupational exposure to pesticides were conducted (Gunther 1980). Entomologists have always been interested in this topic because of their own potential exposure. The first study on human hazard assessment published in JEE concerned the effects of fumigation with hydrocyanic gas (Yothers 1910). A number of studies before World War II commented on the hazards to human health from various pesticides, including arsenic (O'Kane 1916; Huckett 1934;), derris (Wells et al. 1922), and cryolite (Marcovitch & Stanley 1938). Wilson & Holmes (1936) assessed the hazards of eating arsenic-tainted poultry by comparing the residue values obtained from arsenic-fed chickens with levels known to be toxic to humans. Marcovitch & Stanley (1938) also used cryolite residue values on food and the median lethal dose to humans to determine the "factor of safety" for this pesticide.

Chlorinated hydrocarbon insecticides (especially DDT) were initially thought to be safe for humans because large differences in acute toxicities of these compounds were observed between insects and mammals. Human hazard assessments of these compounds were absent from the early entomological literature. On the other hand, several entomologists conducted detailed hazard evaluations of the organophosphate insecticide, parathion (Griffiths et al. 1951; Ashdown et al. 1952; Braid & Dustan 1955; Quinby et al. 1958). Due to the extremely high acute toxicity of parathion and its lack of selectivity, it was deemed responsible for a number of severe injuries and deaths resulting from occupational exposures. Studies showed that absorption of parathion through the skin over several exposure periods created the greatest hazard to applicators and field hands. Metcalf (1951) developed a technique for estimating blood cholinesterase that was useful in the detection of possible exposure to organophosphorus insecticides. Fulton et al. (1955) evaluated the efficiency of respiratory protective devices for agricultural use. Protective clothing, gloves, and respirators had long been known to afford protection against overexposure to pesticides (Metcalf 1951). Entomologists have consistently recommended using pesticides only when necessary and taking proper safety precautions.

## ENVIRONMENTAL CHEMODYNAMICS

The study of the fate and behavior of pesticides in the environment has emerged as a relatively new discipline called environmental chamodynamics (Haque & Freed 1974). Pesticide chamodynamics essentially involves four areas of research:

1. Physicochemical properties of pesticides that influence their behavior in the environment;
2. Mechanisms of the partitioning of pesticides among environmental components (air, water, soil, biota);
3. Attenuation processes affecting pesticide fate (e.g., photodecomposition, chemical and microbial degradation, etc.);
4. Understanding and modeling of environmental transport processes.

The ultimate objective of environmental chemodynamic research is to assess accurately the exposure of target or nontarget organisms to a pesticide or any contaminant. Since exposure to a chemical is largely dependent on its environmental distribution, the ecological impact of pesticides in any ecosystem is directly related to the sum of the chemodynamic processes.

Pesticide chemodynamic research appearing in JEE between 1908 and 1962 included: residue dynamics on plants; translocation into plants and systemic dynamics; metabolism in plants and transformation products; persistence and translocation in soil; volatilization; formulation chemistry; and bioconcentration. The determination of pesticide residues on crops had received a great deal of attention owing to the establishment of tolerances by the Food and Drug Adminstration and the concern about hazards to human health. In contrast, the interest in residue dynamics seemed to be motivated by rapid decreases in insecticidal activity after application. Early studies investigated the effect of fruit growth and climatic conditions on residue losses (Hamilton 1929; Fahey & Rusk 1940). The effect of sunlight and oxygen on residues was also studied (Jones et al. 1933; Gunther 1943), and methods were explored for the inhibition of insecticide decomposition (Gunther et al. 1948). Some studies were concerned only with the dispersion of residues on foliage and their subsequent rates of loss (MacLeod & Sherwood 1937; Gunther et al. 1946; Dawsey & Markwood 1940).

In the 1950's the focus of pesticide research shifted to the study of residue dynamics with respect to the evaluation and elimination of hazards. Translocation of foliar-applied materials into other parts of the plant, such as the fruit, and the actual location of the residues therein were studied (Smith & Clifford 1950; Blinn et al. 1959; Matsumura 1960). Other studies concentrated on the effects of application rate, number of applications, weathering, and crop dehydration in reducing residues (Stansbury & Dahm 1951; Sloan et al. 1951a,b; Dahm 1952; Hopkins et al. 1952a,b; Westlake & Butler 1953; Waites & Van Middelem 1958). Many researchers graphically displayed residue persistence data with the concentration recovered as a dependent variable and the time after application as an independent variable. The resulting curves were biphasic; an initial rapid loss of pesticide was followed by a much slower degradation rate (e.g., Decker et al. 1950; Hopkins et al. 1952a,b; Fahey et al. 1952). Gunther & Blinn (1955) discussed these curves as representing a two-step process in which the rapid initial loss of residue is related to weathering, and the slower loss is related to metabolically induced alterations.

The application of systemic insecticides to soil has been viewed as a relatively efficient and selective method for controlling pests. Questel & Connin (1947) were first to show that the treatment of soil with parathion produced plant tissues lethal to the European corn borer. Terriere & Ingalsbe (1953) showed that potato tubers absorbed chlorinated hydrocarbon insecticides from soil as long as 3 years after the initial treatment. Getzin & Chapman (1959) proved that soil type greatly influenced the amount of insecticide translocated from the soil. Reynolds & Metcalf (1962) showed that there was a direct relationship between the water solubility of a chemical and the amount taken up by a plant.

The metabolism and systemic dynamics of organophosphate insecticides were extensively studied by Metcalf, March, Casida, and their coworkers. Casida et al. (1952, 1954) showed that plants could metabolize octamethylpyrophosphoramide to a toxic, anticholinesterase product. Metcalf et al. (1955, 1957a) and Fukuto et al. (1956) showed that phorate and the isomers of Systox were oxidized in plants to toxic metabolites. Gannon & Decker (1958) demonstrated that aldrin, a chlorinated cyclodiene, was oxidized in plants to the equally toxic epoxide, dieldrin. Metcalf & March (1952) and Metcalf et al. (1954, 1956, 1957b) conducted detailed, comprehensive studies on the systemic dynamics of radiolabeled organophosphates. Radioautographs of whole leaves were used to visualize distribution of the insecticide.

Throughout the 1950's studies proliferated on the persistence of the chlorinated hydrocarbon and cyclodiene insecticides in soil (Fleming & Maines 1953, 1954; Kiigemagi et al. 1958; Young & Rawlins 1958; Lichtenstein & Polivka 1959; Lichtenstein et al. 1960). Little work had been published on the persistence of the organophosphates at that time (Menn et al. 1960). The major concern seemed to be with the accumulation of residues in soil and their possible phytotoxic effects. There was also a need to understand residue dynamics so that control of soil pests could be optimized. Lichtenstein and his coworkers conducted extensive research on the effects of soil type, temperature, moisture, mode of application, and cover crop on pesticide persistence and translocation (Lichtenstein 1958; Lichtenstein & Schulz 1959b, 1961; Lichtenstein et al. 1962). Some work was reported on the adsorption of insecticides by soils (Chisholm & Koblitsky 1943; Getzin & Chapman 1959; Weidhaas et al. 1961) and on volatilization (Harris & Lichtenstein 1961). In most of the insecticide-soil interaction studies, soil organic matter content appeared to be the most significant property affecting pesticide translocation and persistence. Edwards et al. (1957) showed an inverse relationship between soil organic matter content and toxicity.

Several studies proved that insecticides could be oxidized in soil to biologically active metabolites. Gannon & Bigger (1958) and Lichtenstein & Schulz (1959a) were the first to show that aldrin and heptachlor were transformed into the toxic epoxides, dieldrin and heptachlor epoxide. Lichtenstein & Schulz (1960) showed that the transformation was biological and did not take place in autoclaved soils. The organophosphate insecticide, phorate, was also shown to be oxidized in soil or by soil microorganisms to products similar to those found in plants by Metcalf and his coworkers (Ahmed & Casida 1958; Getzin & Chapman 1960).

Several early experiments measured the volatility of insecticide formulations containing nicotine, DDT, and some fumigants in relation to effects on insect control (DeOng 1923; Roark &

Nelson 1929; Fleck 1944). One study reported the contamination of food and air by lindane applied as a surface spray (Siakotos 1956a). Other studies of formulations measured the efficiency of various materials as carriers for different insecticides (Headlee & Rudolfs 1922; Eddy 1926; Weidhaas 1957) and the stability of various spray mixtures (Gunther 1947; Cutkomp 1947).

No studies were found in JEE prior to 1962 that measured bioconcentration factors, but the accumulation of insecticides in nontarget organisms after they had fed on treated forage or after area-wide sprays was studied (Wilson et al. 1946a). Early studies reported the absorption of arsenic by vegetables grown in soils treated with lead arsenate (McLean et al. 1944). Dairy cows pastured in fields sprayed with chlorinated hydrocarbon and cyclodiene insecticides secreted the pesticides in their milk (Entomology Research Division 1959; Gannon & Decker 1960). DDT residues were found in dairy and poultry products from New York farms following widespread aerial spraying for gypsy moth control (Huddleston et al. 1960a). One study showed that leaves from elm trees injected with the organophosphate, Tetram, were toxic to earthworms and rats (Al-Azawi et al. 1961).

## CONCLUSIONS

The publication of *Silent Spring* (Carson 1962) has been credited with informing the general public of the hazards of pesticide use and creating an attitude of enviornmental awareness. The purpose of this historical review of environmental toxicology was to trace the evolution of this environmental awareness from the perspective of the entomological literature. It became clear after reviewing over 200 papers published primarily in the *Journal of Economic Entomology* between 1908 (volume 1) and 1962 (volume 55) that the interest in environmental toxicology evolved from the research efforts of insect toxicologists before and immediately after World War II. JEE, originally published as the proceedings of the *American Association of Economic Entomologists*, served as a continous forum for a multitude of insecticide toxicology studies. The *Journal of Agricultural and Food Chemistry*, published by the American Chemical Society, also served as a forum after 1953.

Today more than 10 journals regularly publish research on environmental toxicology. Many of these journals have existed for less than 15 years. Toxicological research encompasses a great number of environmental contaminants, and researchers are trained in a wide variety of fields. It is pertinent to note that the current and past scientific advisory panels to the U. S. Environmental Protection Agency have had entomologists trained in insect toxicology as members. The combination of strong training in biology and chemistry has enabled insect toxicologists to adapt their research to a wide range of environmental problems that go well beyond the bounds of traditional economic entomology. With considerable foresight Moore (1923) observed, "The economic entomologist should be well grounded in chemistry, especially organic and physical chemistry for the purpose of enabling him to see and solve the problems in connection with the use of insecticides."

In retrospect, it appears that economic entomologists have traditionally been concerned with both the benefits and the risks of pesticide use. The dilemma of the entomologist in balancing crop protection with environmental protection was perhaps best expressed by Dr. George Decker of the Illinois Natural History Survey. In a presentation about DDT residues before the Insect Control Committee of the National Research Council, Decker (1946) said, "The entomologist frequently finds himself in difficult positions. He is expected to assist the farmers by supplying information on the latest and best possible recommendations for the control of insect pests. At the same time, he is obligated to guard against recommending any procedure or treatment that might endanger the life or health of man or beast. In the absence of reliable data, he must proceed with reasonable caution and must at all times avoid being carried away by current waves of public opinion. Today, he must balance the merits of DDT against the hazards that might accompany its use and weigh carefully the evidence on both sides of the equation."

It is incumbent upon insect toxicologists to understand and explain the diverse aspects of the fate and behavior of insecticides in the environment so that they may be used in the most efficient and safest manner possible.

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# Biotic and Abiotic Stresses as Primary and Predisposing Factors Affecting Illinois Trees

D. F. Schoeneweiss, Dan Neely, and E. B. Himelick

Illinois, the Prairie State, is in the heart of the nation's breadbasket. Deep, flat, prairie soils and equitable climate are ideal for the modern, highly mechanized production of row crops. With nearly 12 million acres of corn and 10 million acres of soybeans annually, Illinois is a major agricultural state and is known around the world for high yields. In the face of this intensive agriculture, it is small wonder that the forests and woodlots of Illinois have received only limted attention as valued natural resources. With less than 11 percent of its total acreage forested, Illinois ranks last among states east of the Mississippi in proportion of wooded area (Stewart 1980).

Before 1800, over 40 percent of the state was covered by forest, particularly in southern, western, and northern Illinois and along major rivers (Herendeen & Rolfe 1983). By 1858, the date from which the Illinois Natural History Survey marks its beginning, much of the wooded land had been cleared for farming. As long ago as 1886, members of the State Laboratory of Natural History, a forerunner of the Survey, were voicing concern over the rapid loss of Illinois' trees (Carter 1958). The acreage of forest has continued to decline to the present day due to logging, disease, clearing for cropping, and the development of urban and industrial complexes. Because of the relative scarcity of trees, their protection and preservation in Illinois are of vital concern to its citizens.

## FOREST RESOURCES OF ILLINOIS

The forest resource base in Illinois can be divided into two categories, rural and urban (Stewart 1980). The rural base consists of national, state, county, and private forests; tree plantations; farm woodlots; and windbreaks. The urban base is made up of trees on parkways and private property and trees in municipal and industrial plantings. In rural areas, windbreak trees, which were widely planted after the dust bowl years of the 1930's, have all but disappeared, as have many farm woodlots, due to the increased conversion of acreage to row crops. The resulting loss of fertile topsoil by wind and water erosion on deforested land has become a vital issue facing the state. Of the 3.5 million acres of Illinois forest remaining in 1967, 96 percent was designated as commercial forest, with 93 percent of this commercial portion in private ownership (Stewart 1980). The Shawnee National Forest in southern Illinois totals 277,000 acres, with county forests making up 126,000 acres and state forests only 11,500 acres. Nearly all of the rural forest is hardwoods, predominantly oak (42 percent) and hickory (11 percent).

The extent and value of the urban forest resources of Illinois have not been adequately defined. Community-owned forests in the 55 largest urban areas total over 50,000 acres (Stewart 1980). It has been estimated (Himelick 1976) that there are over 25 million trees along streets and on private property in urban areas of the state. Some idea of the dollar value of urban shade trees can be gained by looking at the cost of the removal and replacement of

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diseased or damaged trees. The mean in-house costs nationwide for municipal tree and stump removal are $140 per tree, with an additional $45 for replacement planting (Anonymous 1982). If the job is contracted, as is commonly done in cities, the mean costs are $208 for removal and $86 for replanting. Removal and replacement take up 43 percent of municipal tree care budgets. It is estimated that in 1980, 57 communities in Illinois with over 25,000 population spent a total of $11,280,000 for municipal tree care (Stewart 1980). If the costs for privately owned trees were added to this figure, the estimate would likely be doubled.

Tree care in Illinois supports several major horticultural industries. Illinois ranks among the top 12 states in the production of nursery stock, including trees, with an estimated wholesale value of over $100 million annually. Many growers import planting stock from other states and export high-quality specimen landscape trees throughout the eastern United States and Canada. Other sizable industries dealing with trees in the state are represented by the Illinois Landscape Contractors and Illinois Commercial Arborists associations. Also directly involved in tree planting and care are the Illinois Department of Transportation, the Division of Forestry in the Department of Conservation, and the many county and municipal governments in the state (Stewart 1980). Thus, trees are an important economic as well as aesthetic natural resource.

## BIOTIC AND ABIOTIC STRESSES

Trees, like all living things, can become weak and sick and eventually can die. Even forest trees growing in a natural habitat are damaged by insects, diseases, and climatic stresses. During the rapid agricultural and industrial expansion of the last century, the nation's forests were viewed by many as inexhaustible supplies of lumber and as natural barriers to agriculture to be cleared so that the land could be put to better use as farmland. This concept was challenged when the chestnut blight fungus appeared in New York State in 1904 and within 30 years virtually eliminated one of the most valued tree species in North America. Since then, several droughts and such pests as the gypsy moth and the oak wilt and Dutch elm disease fungi, have destroyed vast numbers of trees, emphasizing the vulnerability of our forest resources.

### Biotic Stresses

Stresses caused by insects and diseases are classed as biotic (Fig. 1). Nearly all tree species are under constant attack by pests, most of which are endemic and may be present wherever trees are growing. Disease stresses of trees are caused by fungi, bacteria, viruses, mycoplasma-like organisms (MLO), and nematodes (Hepting 1971). Except for crown gall and fire blight (bacteria), elm phloem necrosis (MLO), and pine wilt (nematode plus fungus), the major known biotic diseases of trees are caused by fungi (Carter 1975; Hepting 1971; Himelick 1976). Fungus species that require living plant tissue as a growth substrate are obligate parasites, those that grow on nonliving organic media as well as plant tissue are facultative parasites (Baker & Cook 1973; Wheeler 1975). Parasitic fungi vary considerably in their ability to attack higher plants. Obligate parasites and virulent or aggressive facultative parasites may attack otherwise healthy plants and act as primary stress factors causing disease damage. Weak or nonaggressive parasites cause damage only if plants are predisposed by other stresses (Schoeneweiss 1975b).

Fungal pathogens enter susceptible and resistant host plants with equal frequency (Baker & Cook 1973; Wheeler 1975). Even wound pathogens that cannot penetrate host plant surfaces directly find avenues of entrance through small wounds, cracks, and lenticels that are present on all plants.

Fig. 1. – Biotic stresses as primary factors affecting Illinois trees. (A) Verticillium wilt on green ash. (B) Nectria canker on thornless honey locust. (C) Sporulating cedar-apple rust galls on red cedar. (D) Anthracnose lesions on black walnut.

Consequently, disease outbreaks and epidemics are influenced by environmental conditions of light, temperature, and humidity (Colhoun 1973). If a susceptible host and a virulent pathogen are present and environmental conditions favor infection, disease damage will appear. Disease outbreaks reach epidemic proportions when pathogen inoculum is abundant and large numbers of susceptible hosts are available, as is the case with street and parkway plantings in which species diversity is lacking. Some spore-bearing fungi and certain bacteria are spread from tree to tree by wind and rain, and others are transmitted by animals, primarily insects.

Where pathogens and host trees have coexisted for many years, trees have usually developed resistance to disease through mutation and natural selection. Pathogens introduced into a population of trees that have not developed resistance can cause devastating disease epidemics. In 1934, the Dutch elm disease fungus came into this country from Europe. The American elm, which was widely planted as a parkway tree throughout North America and was also a common woodland species, had virtually no resistance to the fungus. As populations of the European elm bark beetle vector built up, an epidemic of Dutch elm disease began in the east and is still spreading toward the west coast. As already mentioned, the chestnut blight fungus, which spread rapidly by wind- and rain-carried spores, killed nearly all of the American chestnuts within three decades, because the species was uniformly susceptible. This remains the only case on record of a plant pathogen virtually eliminating its host species (Hepting 1971).

## Abiotic Stresses

Physical, chemical, and environmental factors that adversely affect tree health are called abiotic stresses, or physiological diseases (Parker 1965). The most common environmental stress factors are drought, flooding, and freezing temperatures. Man-induced stresses include wounds, toxic chemicals, pollutants, nutrient deficiencies, changes in soil grade and drainage, soil compaction, and loss of roots during transplanting. Trees suffering from abiotic stress may exhibit a wide variety of symptoms (Fig. 2), from the dropping of older leaves to severe wilting, dieback, and eventual death. When damage occurs as a result of these factors without the involvement of a pathogen, the stress exerted is a primary abiotic stress.

Nearly all trees suffer at one time or another from abiotic stress, but there are several critical periods when they are most susceptible to injury. A young seedling or a transplant struggling to establish a root system may be killed by even a short drought. After a tree becomes established, it is usually able to survive all but unusually severe abiotic stresses for many years. Once the tree approaches maturity, however, the root system has ramified throughout the upper layers of soil and attained an increasingly delicate balance with the soil environment or rhizosphere. Abiotic factors, such as drought, flooding, soil compaction, or toxic chemicals, can stress mature and overmature trees and initiate a state of decline (Himelick 1976). Trees transplanted into a landscape setting and those in natural stands that are thinned by building contractors are frequently subjected to conditions that are likely to cause stress. In addition, landscape and parkway trees all too often are planted in disturbed soils where compaction, alkalinity, and poor nutrient status are unfavorable for tree growth. The increased use of herbicides with lawn fertilizers has also damaged many trees in urban areas (Neely & Crowley 1974).

The most critical period in the life of most urban trees is associated with transplanting, when abiotic stresses may become limiting factors in tree survival and performance. All tree planting stock, whether moved bare rooted or with a root ball, loses a major portion of its absorptive root system (Watson & Himelick 1982b). As a consequence, the uptake of water is reduced, and transplants may suffer drought stress even though soil moisture content is adequate for established trees. To decrease weight and save shiping costs, more trees are being moved with tree spades or with small root balls; therefore, the amount of stress they are subjected to is increasing.

## Predisposing Stresses

Although biotic and abiotic factors can, and often do, act as primary stresses affecting trees, it is common for several factors to interact in causing tree damage. When a tree is weakened by one stress so that it becomes more susceptible to another stress, the tree is said to be predisposed (Schoeneweiss 1975b). Trees stressed by drought, flooding, freezing, or other factors often become predisposed to diseases caused by weak or nonaggressive pathogens that are not able to damage nonstressed trees (Schoeneweiss 1981). Most stem cankers, diebacks, and root rots occur on trees that have been predisposed by other stresses, especially recently transplanted trees, which are often in a weakened condition and are predisposed to biotic diseases (Himelick 1976).

The interactions between abiotic and biotic stresses make the diagnosis of tree damage difficult, often requiring an examination of the tree by an expert to determine the cause of the problem and to recommend the most effective prevention or treatment. Plant pathologists at the Illinois Natural History Survey have provided such expertise as a service to Illinois citizens and institutions for over 50 years

## HISTORY OF TREE DISEASE RESEARCH IN ILLINOIS

The involvement of the Illinois Natural History Survey with trees and their diseases is nearly as old as the Survey itself. In 1881, Thomas J. Burrill, who was on the staff of the Illinois State Laboratory of Natural History as well as that of the state university, demonstrated for the first time that a plant disease, fire blight of pear, was caused by a bacterium. He later published articles on fungal and bacterial diseases of several forest, roadside, and street trees (Carter 1958). Stephen A. Forbes, director of the State Laboratory and guiding force in the evolution of the Natural History Survey, reported on a widespread dying of elms in Illinois in 1883 and again in 1912.

Broad interest in the vegetational resources of Illinois led to the creation in 1921 of the Section of Botany, headed by Leo H. Tehon. Shortly thereafter, when elms began to die in many areas of the state, J. C. Carter joined the staff as a full-time plant pathologist to conduct research on the causes and control of tree diseases. In 1935, the name of the section was changed to Applied Botany and Plant Pathology (Carter 1958) and was later shortened to Botany and Plant Pathology.

In the 1930's research in plant pathology focused on disease problems of street and parkway elms. The rapid dying of elms was due to a disease called phloem necrosis, originally thought to be caused by a virus but recently shown to be caused by a mycoplasma-like organism (Carter 1958). Several other elm diseases were studied by Carter, including bacterial wetwood (Carter 1964). The effort devoted to tree disease research in Illinois was increased after the fungal disease known as oak wilt was found here in 1942. By 1950, when Dutch elm disease appeared in Illinois, Survey plant pathologists were actively conducting research on tree diseases, and additional staff was added to meet this new threat to the rural and urban tree resources of the state.

In 1955, plant pathologists scattered through several departments of the University of Illinois were brought together into a new Department of Plant Pathology. Since Survey pathologists were well established in tree disease research at the time and the university pathologists were primarily interested in diseases of agronomic crops, the Survey accepted the responsibility for research on tree diseases, a commitment that continues today.

Over the years, Survey plant pathologists have cooperated in solving tree problems with many other state agencies, including the Departments of Transportation and Conservation and the Bureau of Plant and Apiary Protection in the Department of Agriculture. As a state-supported institution, the Natural History Survey has provided diagnostic and counselling services to all Illinois residents. During the peak years of the Dutch elm disease epidemic in the 1950's and 1960's, several thousand plant specimens were processed annually in the pathology laboratories. With the opening of the university's plant clinic in 1975, much of the specimen load has been reduced or diverted elsewhere; however, Survey pathologists continue to provide the public with diagnostic and counselling services. Nurserymen, landscapers, arborists, city foresters, pest control operators, Christmas tree growers, and private citizens receive willing cooperation in solving their tree disease problems.

In contrast to agronomic crops, involving only a relatively few species of hosts and pathogens, many abiotic and biotic factors affect dozens of species and cultivars of trees. Keeping up to date on tree disease problems requires a continually evolving program of basic and applied research. As one problem is solved, new ones arise and become issues needing attention.

## RESEARCH ON BIOTIC STRESSES AS PRIMARY STRESS FACTORS

Both the initiation and expansion of research projects on tree diseases at the Illinois Natural History Survey from the 1930's through the 1950's were motivated by the sudden appearance and rapid spread of vascular wilt diseases: phloem necrosis of elm in 1930, oak wilt in 1942, and Dutch elm disease in 1950 (Carter 1958).

### Elm Phloem Necrosis

Little was known about phloem necrosis when it was identified in Illinois in the 1930's except that it was thought to be caused by a virus transmitted by the elm leafhopper. Since virus diseases could not be controlled with chemicals and the application of foliar sprays to control leafhoppers on large trees is seldom practical, research efforts were mostly centered on disease diagnosis and the recording of disease spread and development. Accurate Survey records of the urban epiphytotic of phloem necrosis and Dutch elm disease in the Champaign-Urbana communities (Carter & Carter 1974) are of value in predicting potential tree losses in other similar communities if control programs are not initiated early enough.

### Oak Wilt

The American oaks are the most important group of hardwoods in Illinois and furnish more native timber than any other group of broad-leaved trees. Oak species have also been used extensively as shade and ornamental trees. By 1950, the fungus disease, oak wilt, first identified in Illinois in Winnebago County in 1942, was destroying large areas of oak timber in northern Illinois. Intensive studies on the distribution of the fungus in Illinois, potential vectors, and procedures to control its spread were begun in 1951 with a grant from the Cook County Forest Preserve District, later supplemented and eventually replaced with state and federal funds (Carter 1968; Himelick 1958).

Oak wilt disease was found to be present in almost every Illinois county with large areas of native oaks (Himelick, 1958). The sexual and asexual spore stages of the fungus and their role in the life cycle of the fungus were described (Himelick & Fox 1961). Squirrels and various sap-feeding insects were shown to be potential vectors of the fungus (Himelick & Curl 1955; Himelick & Curl 1958) although none proved to be efficient enough to pose a threat of epidemic disease. Survey pathologists found that the most significant spread occurred through root grafts from diseased to adjacent healthy trees, and methods were tested for interrupting these root grafts. Both mechanical trenching and the use of the soil sterilant Vapam to form chemical barriers (see Dutch elm disease) prevented the spread of the fungus through root grafts (Himelick & Fox 1961). Poisoning trees with sodium arsenite or potassium iodide prevented the formation of fungus pads (Curl 1955) from which spores of the fungus could be carried by insect and animal vectors to healthy trees (Himelick & Fox 1961). The disease is now limited to small pockets of timber in which control measures have not been used.

Oak wilt was, and still remains, a potential threat to the predominantly oak forest and woodlots of the state. If an efficient vector appears, Illinois forests would become highly vulnerable to oak wilt epidemics. Therefore, Survey pathologists are keeping a close watch for any sudden increase in the incidence of oak wilt.

### Dutch Elm Disease

In contrast to the oak wilt fungus, the fungus that causes Dutch elm disease, and its bark beetle vector, found conditions in Illinois ideally programmed for disease epidemics. The streets and boulevards of most cities in the Midwest were planted almost exclusively to American elms, which are highly susceptible to the disease. The European elm bark beetle, an introduced species, breeds in dying elms. When the beetle arrived in advance of the fungus, beetle populations built up rapidly on elms dying from phloem necrosis. In 1950, the Dutch elm disease fungus appeared in Coles County and rapidly spread throughout the lower half of the state, where phloem necrosis was prevalent. By 1959, Dutch elm disease was found in all 102 counties of the state (Carter & Carter 1974). This phenomenal spread was much more rapid and extensive than that which had occurred earlier in the eastern states. Consequently, a program was initiated in the 1950's to attempt to find means of controlling the disease or at least slowing down its rapid spread so that communities could replace dying elms over an extended period.

The beautiful colonnades of parkway elms in Illinois cities began dying rapidly in the 1950's from Dutch elm disease. Since the disease appeared to spread from infected trees to adjacent trees along parkways, Survey pathologists made extensive studies of disease progression and found that the fungus also moved from tree to tree through root grafts. Root grafts were so common among parkway trees that up to 100 percent of the trees within 20 feet and 90 percent of the trees within 35 feet of infected trees also became infected (Himelick & Neely 1962). To halt this type of spread, several methods were devised and evaluated for breaking or interrupting elm root grafts. Mechanical trenching proved to be effective but costly. Several soil fumigants were applied by different methods to kill roots and form a barrier between adjacent trees (Neely & Himelick 1965). The most effective treatment found was the injecting of the soil sterilant Vapam, diluted 1:3 with water, into 3/4-inch diameter holes 15 inches deep and 6 inches apart in a line between adjacent elms. Vapam treatments reduced adjacent tree infections by 60 percent in all Illinois cities where it was tested (Neely & Himelick 1965). This method became a standard recommendation for the control of Dutch elm disease in Illinois cities and was subsequently adopted as a control procedure in other states.

Control strategies were also devised and tested to prevent or reduce the overland spread of the fungus by bark beetles emerging from brood galleries in diseased elms. Over 1 million beetles had been estimated emerging from a single dying elm; therefore, strict sanitation in the form of the prompt removal and destruction of dying trees and branches became an essential component of any effective control program. Unfortunately, few communities were able to organize and fund community-wide control programs until many trees had already been lost to the disease. The biggest problem for communities where elms were dying was that the prompt removal of dying trees was essential to contain the disease epidemic, but sufficient funds and manpower for tree removal were simply not available. To help alleviate this situation, Survey pathologists developed a technique based on previous oak wilt research in which either sodium arsenite at the rate of 100 g/l of water or potassium iodide at the rate of 500 g/l was placed in axe frills at the base of a tree (Himelick & Neely 1961). This treatment caused such rapid tree death that the tree did not become suitable for beetle breeding. The treatment gave almost complete prevention of beetle colonization and allowed communities to remove dead elms at convenient times while maintaining an effective control program.

With the advice and recommendations of Survey pathologists, 55 Illinois cities had begun control programs for Dutch elm disease by 1957 (Neely 1967). The basic program included strict sanitation and the application of DDT sprays. When DDT was banned in 1968, more than half of the cities dropped their control programs, while the remainder substituted the less effective insecticide methoxychlor for DDT. In cities with no control programs, over 90 percent of the elm populations were lost to disease by 1966 (Neely 1967), and those that dropped their programs soon lost most of their remaining elms. The 21 cities that have continued control programs through 1982 have retained from 30 to 50 percent of their original elm population, allowing the gradual replacement of dying elms with other tree species over a 25-year period (Neely 1984). Control strategies developed at the Survey have served as models for community-wide Dutch elm disease control programs in many parts of the country.

Another phase of research which found practical application was a comprehensive study on the spread of the Dutch elm disease pathogen within infected elms. When inoculations were made at the base of the trunk, the fungus was recovered at a height of 6 feet in 3 days, and at 6 days was present in the tops of trees 4 to 5 meters high. In contrast, twig inoculations, simulating beetle feeding transmission, resulted in downward movement of only 2 cm per day, and it was weeks or months before the fungus reached the main stem (Neely 1968). Unless a main stem was reached in the first year of inoculation, the fungus became localized. Using this information, Survey pathologists found that if infected branches were surgically removed before trees showed more than 5 percent wilt (flagging) symptoms, up to 65 percent of the infected trees could be saved (Himelick & Ceplecha 1976). Therefore, early detection and prompt pruning were included in control recommendations.

Many additional studies on Dutch elm disease were conducted, including a survey of resistant species and cultivars of elm. Of 13 species and subspecies of *ulmus* on the University of Illinois campus, only *U. americana L.*, *U. rubra* Muhl., and *U. thomasi* Sarg. were lost to the disease (Neely & Carter 1965). Unfortunately, nearly all parkway trees on the campus and in the twin cities of Champaign-Urbana were *U. americana*. Of the original population of 14,103 American elms, only 47 trees remained in 1972 (some of these have since succumbed to disease); the rest were killed by either phloem necrosis or Dutch elm disease (Carter & Carter 1974). This loss resulted from the lack of any control program in the twin cities. Fortunately, other communities in the state that followed Survey recommendations were able to retain many of their elm trees.

### Verticillium Wilt

Verticillium wilt is a vascular disease caused by a soil-borne fungus, *Verticillium dahliae* Kleb., and is the only vascular tree disease that affects a wide range of unrelated annual and perennial plant species (Himelick 1969). In Illinois, the disease is rare among forest trees, but it has become increasingly prevalent in ornamental plantings (Fig. 1A). Presently, 60 species of trees and shrubs are known to be susceptible (Himelick 1969). There is evidence that the fungus varies in virulence, and the indiscriminate movement of nursery stock from one state to another has resulted in distribution of the more virulent strains to areas of Illinois where they were not previously present.

Survey pathologists have researched the biology, control, and host range of *Verticillium* over many years. Diagnosis is difficult because trees weakened by root infection usually decline and become more susceptible to the effects of other stresses. Attempts at chemotherapy with fungicides have been unsuccessful. Feeding and watering infected trees are the only treatments that have proved helpful in extending the longevity of trees having Verticillium wilt.

## OTHER BIOTIC DISEASES AS PRIMARY STRESS FACTORS

### Sycamore Anthracnose

American sycamore, a common river-bottom species in the eastern half of the United States, has been widely planted as a shade tree on parkways and private property. It is a hardy, fast-growing species, but its value as an urban shade tree is limited by a fungal disease known as sycamore anthracnose (Himelick 1962; Neely 1976). Occasionally, sycamores appear quite healthy throughout the summer, but in most years anthracnose damage ranges from moderate to severe defoliation early in the growing season. In response to numerous requests from nurserymen, arborists, and homeowners for disease control recommendations, pathologists at the Natural History Survey conducted research on the biology and control of this disease.

A taxonomic study of the pathogen revealed that it was distinct from the oak anthracnose fungus (Neely & Himelick 1967), and it was established as a separate species (Matteoni & Neely 1979). The disease cycle on sycamore was found to be composed of several stages (Himelick 1962). The fungus overwinters in current-season twigs and causes bud, twig, and shoot blight symptoms following bud break in the spring. It also forms stem cankers in which spores are produced that serve as a source of new infections. During late spring and summer, spores infect leaves, causing the leaf-blight stage. The fungus invades leaf petioles and grows downward into the stem, where it remains over the winter. Since the fungus spends most of its cycle within petiole and stem tissues, the disease is difficult to control with surface-active fungicides. Mercury fungicides, which penetrate plant tissues and act as localized systemics, gave good control of anthracnose, but mercuries have been banned from use because of their high mammalian toxicity. No other foliar fungicides tested have been effective; however, pressure injection of trees with the fungicide Arbotect has given good control for as long as 3 years (Himelick & Duncan 1982).

Research on the anthracnose cycle led to the development of a predictive model for disease outbreaks. Pathologists found that temperature controls the severity of shoot blight, the most damaging stage of the disease (Neely & Himelick 1963a). If mean daily temperatures during the 2 weeks following first leaf emergence average less than 13°C (55°F), severe damage occurs. When temperatures from 13° to 16°C (55° to 60°F) occur, damage is moderate, and at temperatures over 16°C (60°F) no shoot blight appears. Cool temperatures in both fall and spring favor fungal growth in twigs. After several years of testing and refinement, this model has proved to be quite accurate in predicting anthracnose severity and is useful in decision making as to if and when fungicides should be applied for disease control.

## Walnut Anthracnose

Black walnut (*Juglans nigra* L.) has long been a highly valued native tree in Illinois, both as a source of cabinet-grade and veneer lumber, and as a producer of edible nutmeats. Walnut plantations have sprung up throughout the southern part of the state as farmers and other landowners have rushed to take advantage of the increasing demand and rising prices for walnut products. Because of nationwide interest in walnut, the U.S. Forest Service made funds available for research on walnut culture and pest control. A Survey plant pathologist received a grant to study control measures for walnut anthracnose (Fig. 1D), the most serious disease of walnut (Neely 1979).

Since effective control measures for a plant disease depend upon a thorough knowledge of the growth habits and life cycle of the pathogen, studies were conducted on the anthracnose fungus, using artificial media in the laboratory and host plants in the field and greenhouse. Detailed information was obtained on pathogen growth and sporulation (Matteoni & Neely 1979) and on host susceptibility at different growth stages (Black & Neely 1978a).

Wide variation was recorded in resistance to anthracnose among various species and hybrids within the genus *Juglans*, with a tendency toward greater resistance when trees are producing rapid growth (Black & Neely 1978b).

Results of fungicide trials showed that several compounds gave good control of walnut anthracnose, the best being benomyl (Benlate) applied as a foliar spray. Two applications are required, the first in late May to control ascospore infection and the second in early July for conidial infection (Neely 1979). Since rapidly growing trees appeared to be more pathogen resistant, various fertilizer combinations were applied to plantation walnuts. The application of nitrogen, at the rate of 3 kg N/ha of soil surface, resulted in a 60-percent decrease in defoliation by the end of the season (Neely1981). Consequently, Survey plant pathologists now recommend a combination of fungicide sprays and fertilization for maximum control of walnut anthracnose.

## TREE SELECTION FOR DISEASE RESISTANCE

Control of biotic tree diseases may involve several methods or approaches. These include chemotherapy, surface and soil applications of fungicides, sanitation, fertilization to promote tree vigor, and selection and breeding (Carter 1975). Since the breeding of trees requires many years, selection among available types is far more common than breeding in the development of disease-resistant trees (Carter 1966). In most cases, species and varieties within a genus vary in resistance to biotic pathogens (Bingham et al. 1971); however, accurate information on genetic resistance in trees is often lacking due to the considerable time and effort needed to obtain this information. Survey pathologists working with tree diseases over the years have made surveys and kept records of host resistance to several of the common tree diseases. Most of these studies have been conducted in cooperation with the Morton Arboretum at Lisle, Illinois, where a wide range of tree species and varieties is located. Lists have been published of junipers resistant to twig blight (Schoeneweiss 1969) and cedar rusts (Himelick & Neely 1960) and of varieties of horse chestnut and buckeye resistant to leaf blotch (Neely & Himelick 1963b). Results of surveys and inoculation experiments have been combined into a list of woody hosts susceptible to the Verticillium wilt fungus (Himelick 1969). This information is valuable to growers and propagators in selecting and selling trees that are resistant to diseases.

## DISEASE CONTROL WITH FUNGICIDES

With the development of organic pesticides after World War II, the most common method of disease control was the application of fungicides. However, the overuse and abuse of such pesticides, combined with increased environmental awareness, has led in recent years to the banning or restriction of pesticide usage. The amount of scientific data now required before a fungicide can be labeled for a specific use imposes a particularly severe constraint on the control of tree and shrub diseases, which are considered minor uses. With funds provided by the federal program for minor-use pesticides, Survey pathologists have tested many fungicides on ornamental plants and have submitted data on phytotoxicity to aid in obtaining label clearance so that these compounds can be legally used for disease control on nursery and landscape plants.

### Fungicide Bioassay Procedures

To select a suitable fungicide to control a plant disease and to determine the proper timing and number of applications needed, it is necessary to know at what rate of application the fungicide is effective, whether it will remain active on or in the host, and whether the activity will persist or be lost through weathering. These data are usually obtained through the use of bioassays in fungicide screening tests. Because most bioassays gave inconsistent results, Survey plant pathologists developed a cellophane disc technique, which can detect small amounts of fungicide (as low as 0.01 ppm) and may be used in the field as well as in the laboratory (Himelick & Neely 1965). This technique is simple, fast, and economical, and it is now used to determine whether a fungicide kills or merely inhibits disease organisms and whether it will persist on or in plant tissues long enough to give good disease control.

### Chemotherapy

The term chemotherapy refers to the internal treatment of infected plants with chemicals to cure disease or arrest further infection. The field of chemotherapy for tree diseases is in its infancy. Injection into the soil and direct injection of systemic fungicides into the vascular system of trees have been used in attempts to control vascular wilt diseases, but results have often been either negative or inconclusive. Survey pathologists developed a pressure-injection apparatus with which they have injected as much as 110-150 l of dilute systemic fungicides into several tree species (Himelick 1972). American elms in the early stages of Dutch elm disease have been saved by pressure injections of the fungicides Benlate and Arbotect (Himelick 1972), and good control of sycamore anthracnose for up to 3 years has been achieved with the injection of Arbotect (Himelick & Duncan 1982). We expect that other serious diseases of shade and ornamental trees will be controlled by pressure injection in the future with new systemic fungicides.

## RESEARCH ON ABIOTIC STRESSES AS PRIMARY STRESS FACTORS

Although damage symptoms on trees are often attributed to infectious diseases, the fact is that much damage to trees and other plants is caused by abiotic stresses (Levitt 1980a, 1980b; Parker 1965). Since Survey tree pathologists are concerned with the protection and preservation of trees in general, many research projects have been conducted on abiotic stresses.

### Herbicide Damage

The increased use of herbicides for weed control in both rural and urban areas of Illinois is reflected by a higher incidence of damage on sensitive tree species. Rural windbreaks and woodlot trees are being injured by herbicides used on crops, while urban trees are showing the effects of weed-and-feed lawn fertilizers which have become quite popular for the control of weeds in turf grasses (Fig. 2B). A recent study at the Survey revealed that the herbicide dicamba, commonly incorporated with lawn fertilizers, consistently caused significant damage to trees (Neely & Crowley 1974). Tree species differed in sensitivity to this compound, and the extent of damage varied with soil type and the amount of spring rainfall. Pathologists at the Survey have cautioned against the use of dicamba in the vicinity of trees and other woody plants.

### Iron Chlorosis

Yellow foliage and slow growth are typical of many tree species planted along streets and around homes where the original topsoil has been removed or mixed with subsoil. The average urban soil has relatively poor physical, chemical, and biological characteristics. In Illinois, chlorosis (yellow foliage) is a common physiological stress on pin oak (Fig. 2D) and to a lesser

Fig. 2. – Abiotic stresses as primary factors affecting Illinois trees. (A) Oak decline in northern Illinois. (B) Injury from lawn herbicide on yew. (C) Loss of roots during transplanting. (D) Iron chlorosis symptoms on pin oak leaves.

extent on sweet gum, white oak, bald cypress, river birch, red maple, and hackberry. Several Survey pathologists have investigated the cause and control of the chlorosis problem.

Soil tests from areas of chlorotic trees have consistently shown that chlorosis is generally associated with pockets of alkaline clay soils, quite common in urban areas in the northern part of the state (Schoeneweiss 1973). The yellowing of leaves, with veins remaining green, is a typical symptom of iron deficiency and can be corrected by treating plants with certain iron-containing compounds if the iron is in the proper form (Wallace 1971). Field research has centered around both soil injection and direct trunk implantation of iron compounds. Trunk implantations with ferric citrate and ferric ammonium citrate were found to be effective on pin oak, red oak, and swamp white oak; cypress; and sweet gum (Neely 1973; Himelick & Himelick 1980). These compounds are now commercially available in Medicaps® and are being used nationally to correct chlorosis by commercial arborists, nurserymen, and operators of fruit orchards. Applications of inorganic iron compounds to the soil, prior to the 1960's a standard recommendation, was totally ineffective in the alkaline clay soils of Illinois. However, pressure injection of liquid organic compounds, known as iron chelates, corrected even advanced stages of chlorosis in highly alkaline soils for 3 or more years (Schoeneweiss 1973). Either treatment may be used for iron chlorosis in Illinois.

## Nutrient Deficiencies

Many urban trees planted in disturbed soils have poor growth characteristics due to deficiencies of nutrients. Although the fertilizing of parkway, street, and private-property trees in cities is a common practice, most fertilization recommendations are based on studies of crop plants or turf grasses and have not been evaluated on trees. To find out what nutrient materials and methods of application are best for promoting tree growth, Survey pathologists applied several different fertilizer combinations by several methods to experimental blocks of shade tree species at five locations throughout Illinois. They found that trees responded to soil applications of nitrogen fertilizers and that the response was directly related to nitrogen content regardless of how the fertilizer was applied or other nutrients present (Neely & Himelick 1966). Ammonia, ammonium sulphate, urea, and ureaform were equally effective, based on equal nitrogen content. Optimum growth response was obtained with young, newly established trees when fertilized in April at the rate of 3 Kg N/ha of soil surface (Neely & Himelick 1966; Neely et al. 1970). Growth response varied with tree species, but all treated trees were healthier than untreated controls. Proper fertilizing of urban trees enhances tree vigor and helps trees resist attack by many stress-related disease and insect pests.

## Transplanting Stress

The bulk of the root systems of trees are lost when they are dug and moved from the nursery to a planting site (Watson & Himelick 1982a). Because of high labor costs for hand balling nursery stock, more trees are now being moved with large mechanical tree spades, which cut off a larger portion of the root system than does hand balling (Fig. 2C). Consequently, losses of transplanted trees from damage caused by abiotic stresses (Himelick 1976) and predisposition to biotic stresses (Schoeneweiss 1965, 1966) have increased.

Survey plant pathologists recently conducted a 4-year study on the patterns of root distribution and regeneration of seven species of trees transplanted with a commercial tree spade (Watson & Himelick 1983). The study was conducted in the Survey arboretum at Urbana, where core samples from root balls and the soil could be taken to the laboratory for detailed examination. Data were collected on root carbohydrate content, vertical and horizontal distribution of the original root system at the time of digging, and regeneration of fibrous feeder roots after transplanting.

They found that as much as 98 percent of the original root system was lost during digging, yet the survival rate after 1 year was 97 percent, due to careful maintenance of the trees after transplanting (Watson & Himelick 1982b). Because the tremendous loss of roots caused many trees to become severely water stressed in midsummer, frequent irrigation was essential for survival. New fibrous roots formed at the severed ends of the roots at the edge of the root ball and were most numerous in the uper 10 cm of soil. Root regeneration was proportional to carbohydrate content, which was lowest during the period of bud break and new shoot growth in early spring, indicating that trees should not be moved until new growth has matured or, preferably, after the onset of dormancy in the fall.

Results of this study were compiled in a transplanting manual, published by the International Society of Arboriculture (Himelick 1981), for the purpose of developing uniform transplanting procedures. Use of this information should help to reduce losses of urban shade and ornamental trees after transplanting.

## Oak Decline

Several thousand large, established oaks have died or are in various stages of decline on private and public property in cities adjoining Lake Michigan (Fig. 2A). Aerial reconnaissance, using high-resolution photography, has shown extensive loss of valuable trees in many of the urban areas north of Chicago, where oak is the predominant shade tree (Himelick 1976). Although declining trees have been attacked by disease and insect pests, the death of high proportions of the root systems, caused by alternating periods of excess soil moisture and drought, is responsible for the decline.

Through field research it was demonstrated that a 5- to 10-cm layer of wood chips placed over the root area and the addition of surface-applied fertilizer were highly beneficial in restoring the vigor of delcining trees. Fine root development more than doubled in the top 15 cm of soil among trees that were mulched in this manner. Large, 75- to 100-year-old oaks also showed measurable response in greener foliage compared with that of untreated trees.

## STRESS PREDISPOSITION

Many of the biotic diseases of trees that cause significant damage, such as the stem cankers, diebacks, and root rots, only appear on trees that have been predisposed to disease by abiotic stresses (Fig. 3) (Schoeneweiss 1981). Others, such as Hypoxylon canker on aspen and Armillaria root rot of maple and oak, that cause minor injury to vigorous trees may become much more damaging to trees under stress (Schoenweiss 1978). Interactions between abiotic and biotic stresses have long been recognized, yet few studies had been conducted until recently on stress predisposition in woody species. Environmental stresses that occur under field conditions are both highly variable and unpredictable, making it difficult to obtain reliable data on stress-disease interactions from field studies. Most of the useful information has come from studies on controlled stress research at the greenhouse and growth chamber facilities of the Illinois Natural History Survey. Although many different stresses may act or interact in predisposing trees to diseases, research thus far has been concentrated on drought, freezing, and defoliation stresses.

### Drought Stress

The influence of drought, or water stress, as a predisposing factor in stem canker diseases of trees was investigated by placing potted tree seedlings in various stages of wilt into a specially designed humidity cabinet under equi-

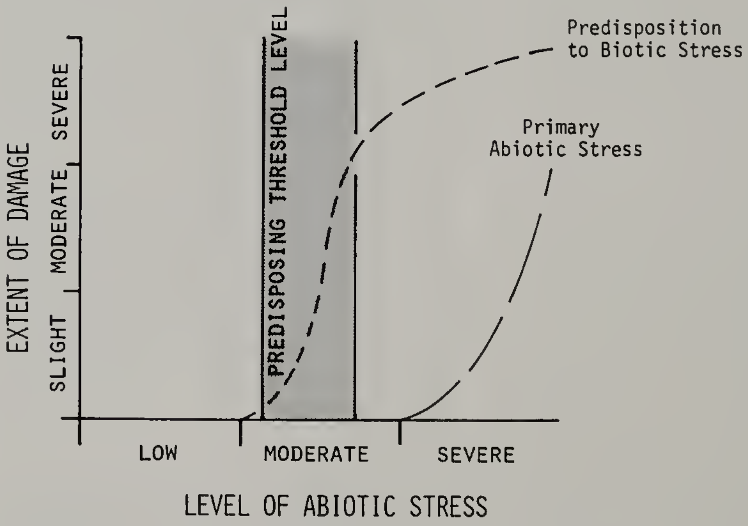

Fig. 3. – The extent of primary damage caused by abiotic stress compared with the extent of biotic disease damage resulting from stress predisposition at increasing levels of abiotic stress severity. Trees may become predisposed to infectious disease organisms at moderate levels of stress, while direct or primary stress damage usually appears only on severely stressed trees.

librium conditions of high humidity, constant temperature, and reduced light (Schoeneweiss 1975a). Under these conditions, plant water potentials became stable, and the level of water stress was correlated with the development of stem cankers caused by weak or nonaggressive pathogens (Crist & Schoeneweiss 1975; Schoeneweiss 1975b, 1978, 1983). These studies revealed that woody stems became predisposed to disease when plant water potentials fell below a threshold level of −12 to −13 bars (1 bar = 0.97 atmosphere) and that disease development increased with increasing stress severity (Crist & Schoeneweiss 1975). The predisposing level would be considered moderate stress, as most tree species do not show signs of wilting at this level. In the field, water potentials of trees may fall well below the threshold level on a hot, windy day yet recover at night without causing predisposition. For predisposition to occur, plant water potentials must remain below the threshold level for several days before trees appreciably lose disease resistance (Wene 1979). Trees regain resistance several days after the stress is relieved. Most trees are under prolonged water stress during droughts and after transplanting and should be irrigated regularly at these times to prevent predisposition to biotic disease.

## Freezing Stress

The predisposing effect of freezing stress was studied by placing dormant potted tree seedlings in a programmable walk-in freezer and lowering the chamber temperature to below freezing (Schoeneweiss 1974, 1977). Stems inoculated with canker fungi became predisposed to disease when stem temperatures exceeded a threshold degree, usually around −20 °C (−13 °F). Predisposed plants regained resistance within 1 to 2 weeks after stems were thawed (Wene 1979). Again, the level of stress resulting in predisposition was considered moderate, since no direct injury was apparent, and frozen plants that were not inoculated were indistinguishable from unfrozen controls after growth resumed (Schoeneweiss 1981).

## Defoliation Stress

Loss of foliage during the growing season reduces the photosynthetic capacity of trees and may weaken them sufficiently to predispose them to biotic diseases (Schoeneweiss 1981). Defoliating insects, like the gypsy moth and cankerworms, have been followed by the decline and death of trees due to canker, dieback, and root rot fungi. Controlled studies at the Survey, where tree seedlings were manually defoliated, resulted in predisposition to canker fungi when plants were defoliated beyond a threshold period of several weeks (Crist & Schoeneweiss 1975; Schoeneweiss 1967). If allowed to refoliate, seedlings recovered without ill effects in the absence of biotic pathogens.

## Plant Tissues Affected by Different Stresses

Although many environmental stresses predispose trees to weak biotic pathogens and all seem to require some threshold level that must be exceeded, the effects of stress on plants may be quite different. Drought, defoliation, and most other stresses weaken the entire plant and may predispose any portion of the plant to attack (Schoeneweiss 1981). In contrast, freezing stress predisposes only that portion exposed to temperatures below the threshold degree (Wene & Schoeneweiss 1980). Freezing stress has a greater effect on older wood tissues, while other stresses predispose bark and sapwood (Schoeneweiss 1981). Pathogens also colonize the xylem of stems stressed by freezing to a much greater distance beyond canker margins than they do with other stresses. In pruning diseased stems to help stressed trees recover, it is helpful to know what environmental stress was involved.

## Stress-Related Pathogens

The appearance of stem cankers, diebacks, and root rots is usually an indirect effect of predisposing abiotic stress. Some of the organisms that cause the diseases are present on planting stock imported from other states, but most are common saprophytes of woody tissues and are widely distributed. These pathogens are often referred to as "secondary" organisms, and their role in causing damage has been disregarded; however, trees recover from stress without ill effects in the absence of these pathogens. Therefore, they should be thought of as essential components of the damage resulting from stress (Schoeneweiss 1981). As different environmental stresses may differentially predispose tree species to disease, information derived from controlled studies with specific hosts and pathogens in combination is useful in formulating recommendations for disease prevention or treatment. Outbreaks of diseases resulting from stress predisposition may not be noticed for days, months, or even years after the stress has been relieved. Climatic data and the cultural history of a tree may provide clues to the factors contributing to disease damage.

## CURRENT RESEARCH ON BIOTIC AND ABIOTIC STRESSES

Given the number and complexity of biotic and abiotic stresses and the wide range of species and cultivars of trees grown in Illinois, tree disease research is a continually changing and evolving process. Even in a paper of this size, many of the research projects conducted by Natural History Survey plant pathologists over the years must of necessity be omitted. In this section we briefly look at some of the major problems under investigation at the present time.

### Histology and Biochemistry of Predisposition

When a tree is predisposed to disease by stress it becomes more susceptible to another stress, in most cases a biotic pathogen (Schoeneweiss 1975b). Since nonstresed trees are able to resist attack by most pathogens, a histological or biochemical change most likely occurs in the predisposed host before infection (Bell 1981). Which mechanisms change or break down during predisposition is a controversial subject about which little is known. Research is currently under way at the Survey to help answer these questions.

Weak or nonaggressive stem-canker fungi are examples of biotic agents that only attack trees that have been predisposed to disease. When stems of nonstressed and stress-predisposed tree seedlings, inoculated with canker fungi, were examined with the light and scanning electron microscopes, no morphological barriers or deposits were found that could account for resistance to fungal growth in vascular tissues (Wene 1979). In resistant stems, the canker fungi appear to be inhibited biochemically or degraded by host enzymes (McPartland & Schoeneweiss 1984). More research is needed to understand which mechanisms operate and how trees become predisposed. Once the resistance mechanisms are identified and characterized, it may be possible to select or breed trees less sensitive to predisposing stress or to apply treatments to enhance the expression or genetic resistance to stress.

### Wound Healing

Tree wounds serve as avenues of entrance for disease and decay organisms. Although much has been written about wound healing and wound treatment, few recommendations have been based on sound research data. In studies being conducted on the healing of various sizes and shapes of wounds on different tree species, pathologists at the Natural History Survey have found that wound closure is directly related to radial stem growth. Large wounds close more per unit of radial growth than do small ones, but wounds on fast-growing trees within a species close less per unit of growth than those of slow-growing trees (Neely 1983). Some tree species are more efficient in wound closure than others. If trees are maintained properly, wounds of less than 1.2 cm in diameter, such as those resulting from trunk injections, close within a year. Tests are under way on the closure and healing of branch pruning wounds, common on nursery and landscape trees. Data from this study will provide a sound basis for recommendations on wound treatment.

### Modeling of Cedar Rust Infections

Cedar rusts are common and troublesome diseases of crabapple and hawthorn. Using pathogen and environment as the variable functions, we have developed models to predict the likelihood of infection by the cedar-apple and cedar-hawthorn rust fungi. These models will be tested against natural field infection to evaluate their accuracy in forecasting disease epidemics. If accurate, they would be of considerable value as a basis for effective fungicide recommendations.

### Tree-Grass Competition

In most urban parkway and landscape settings trees are surrounded by turf grasses. As a result, these trees are often stressed due to competition between tree and grass roots for available water and nutrients. Pathologists at the Survey are collecting data on growth rates of trees in experimental plots with and without living turf cover and with and without supplemental fertilization. The aim is to determine whether killing the turf with herbicides will improve tree vigor. Hopefully, effective means of preventing or reducing stresses in landscape trees will be derived from this study.

### Honey Locust Decline

Of the many declines that occur on shade and ornamental trees, one of the most serious is the decline of the thornless honey locust. Because honey locust has been the preferred species used to replace elms lost to Dutch elm disease, it has been widely planted in urban areas of Illinois, and decline has become a prominent problem. Isolation and inoculation studies with fungi from declining trees indicate that *Thyronectria astro-americana* (Speg.) Seeler is a major cause of decline of older, established locust (Stim & Himelick 1981). Symptoms include cankers that girdle twigs and branches and, in advanced stages of decline, large, elongated cankers that develop on the trunk. An insect borer is associated with the canker and may be a vector of the fungus responsible for the damage. Symptoms appear particularly during periods of drought. Studies are in progress to determine if various cultivars of honey locust show resistance to the fungus.

### Pine Wilt

For the past 5 years, a rapid decline of pines has been observed in both urban areas and pine plantations in Illinois and neighboring states. The incidence of this disease increased dramatically during 1980 and 1981, particularly among Scotch and Austrian pines in Illinois, and in some areas reached epidemic proportions. Many nurserymen and growers of Christmas trees have become concerned about the potential economic loss that could occur if the disease continues to spread. The pine wilt nematode, *Bursephalenchus xylophilus* Mamiya & Kiyohara, and a blue-stain fungus, *Ceratocysts ips* (Rumb.) C. Moreau, appear to be closely associated with the disease (Himelick 1982). An international conference on pine wilt was held recently in Illinois, and a cooperative research effort involving entomologists, nematologists, and plant pathologists from the Natural History Survey and the University of Illinois has been initiated to investigate various aspects of the pine wilt syndrome.

## OUTLOOK FOR ILLINOIS TREES

In spite of research efforts by Natural History Survey plant pathologists, damage caused by biotic and abiotic stresses to Illinois trees is likely to increase through the foreseeable future. Urban trees, in particular, are being neglected because of high maintenance costs. Frequently, more nursery stock is moved with tree spades or grown in containers; in both cases, root systems are often inadequate to assure tree health after transplanting until new roots are established.

Modern farming practices in Illinois, particularly the application of large quantities of herbicides and the plowing of every available square foot of land for row crops, are highly unfavorable to tree health. As a result, rural windbreak and woodlot trees are in poor condition, and many are showing signs of decline.

While stresses are becoming more prevalent as factors affecting Illinois trees, the demand for trees in the state is increasing. Continuing urbanization is creating a greater demand for more shade and ornamental trees for beautification and as noise and pollution filters. The tremendous loss of topsoil to erosion on farm fields may stimulate new interest in windbreak plantings. Tree plantations for the production of biomass as an energy source and for windbreaks are becoming popular. Reforestation of mine spoils and marginal land is being funded at the state and federal levels. All of these factors are contributing to a greater demand for tree planting stock.

The chances for the introduction of a disease organism that could result in a tree disease epidemic has increased in recent years. Many of the new cultivars grown in Illinois nurseries are propagated in other regions of the country and are imported as planting stock along with the pathogens that occur in those regions. Under Illinois conditions, some of these pathogens will undoubtedly become serious threats.

For these and many other reasons, biotic and abiotic stresses affecting Illinois trees will continue to be issues requiring attention from Natural History Survey plant pathologists. Information from both basic and applied research will be needed to meet these issues.

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# Morning Session Summary

Catherine E. Eastman and Marcos Kogan

The Illinois Natural History Survey, as envisioned by its first chief, Dr. Stephen A. Forbes, was to concern itself not merely with the cataloging of organisms and their distribution in Illinois, but also with the study of the relationships of organisms with their environment (Mills et al. 1958; Hays 1980). The presentations in this symposium today indicate that such studies are still a primary focus of Survey research in keeping with the finest work of our sister biological research institutions and universities.

The environment within which organisms must exist has changed considerably since the early days of the Survey. For example, one has only to look at the landscape of central Illinois to understand the impact that the needs of an increasing human population have had on our own environment and that of other organisms. With the change from marshy prairie and forested hills to drained, plowed farmland well under way in the 1850's, the diverse vegetation well adapted to a prairie environment was replaced by an overwhelming dominance of two plant species – corn and wheat. Such is the case today, although soybeans have replaced wheat in acreage. Monoculture techniques and plant breeding programs have changed the chemical and physical defenses of plants, and soil, air, and water pollutants have made plants more vulnerable to attack by herbivores and disease agents. Pesticides applied to supplement natural plant defenses are yet another environmental element affecting target and nontarget organisms alike. The growth of cities and industry has affected the environment as well by displacing the original plant cover and by releasing enormous amounts of industrial and urban wastes. Thus, we as biological researchers must concern ourselves with problems associated with inherently unstable agroecosystems, with the reduction of suitable habitats and the consequent decline of wildlife populations, and with the difficulties in determining basic biological relationships among organisms in an environment increasingly subject to human manipulation.

The presentations in this symposium are examples of the challenges presented to researchers investigating complex biological systems. In a broad sense most of the talks this morning have been concerned with stresses affecting plants and plant defense biology. Such stresses include herbivore injury, infections by disease agents, competition with other plant species, and a range of abiotic factors, among them temperature and moisture extremes. Stress from one source, such as frost damage or insect feeding, may make the plant more vulnerable to other stresses, such as invasion by pathogenic organisms.

It is in response to the net selective influences that are exerted by these stresses that plant defenses are evolved. In the last 25 years the defensive properties of plant production of secondary metabolites have received increasing attention. The roles that these compounds may play in the producer plant's environment may be quite complex (Rosenthal & Janzen 1979). For example, flavonoids may serve both to screen plants from ultraviolet radiation and to attract pollinators. Phytoalexins presumed to be produced by plants in response to invasion by bac-

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teria or fungi have also been shown in recent work by Survey researchers to deter feeding by the Mexican bean beetle. And some metabolites, such as the cucurbitacins, which are repellent or outright toxic to many herbivores, may also serve as feeding excitants for other phytophagous species. Yet despite the importance of this line of research, a plant's particular chemical profile alone cannot explain plant-herbivore interactions. The microclimate and the types of carnivores present in the plant's environment also contribute to the degree of suitability of a plant or plant part as a host for a particular herbivore.

Pesticides are superimposed on plant defenses when such defenses are deemed inadequate for crop production goals. Their effect in the environment ripples out from the immediate target pest on the host plant to include non-target organisms and for varying distances in the host plant's abiotic environment. Yet the stability of these pesticides often is dependent on that same environment, which determines whether the pesticide will be subject to microbial or ultraviolet degradation or whether it will persist for months or years in a biologically active form.

That astute observer of scientific endeavor and human nature, Mark Twain, is reported to have said that "Researchers have already cast much darkness on the subject, and if they continue their investigations, we shall soon know nothing at all about it." The pursuit of the principles underlying biological relationships often seems to uncover more questions than answers. But those who are both charged and blessed with the task of conducting such investigations can seek comfort in the knowledge that each attempt sheds a little more light on the nature of these relationships and of life itself.

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# Long-term Biological Research In a Rapidly Changing Environment

Lorin I. Nevling, Jr.

This is a great weekend in Illinois for those interested in plants and animals. This morning the Field Museum opened *Plants of the World,* the largest permanent exhibition of plant models ever presented. At this time, just a few miles from here, the Board of Trustees of the Pacific Tropical Botanical Garden sits in session. Tomorrow, the Chicago Botanic Garden in Glencoe will dedicate a magnificent bronze statue of Linnaeus, perhaps the single most influential person in the history of systematic biology. The most significant event, however, is that in which we have the honor to participate – recognition of 125 years of service by the Illinois Natural History Survey to the people of Illinois.

As with many great institutions, the Survey had no precise beginning but evolved through time. Clearly, its genesis began with the proposal that a Natural History Society of Illinois be organized at the Illinois State Normal University. In June of 1858, the society was formed, its constitution providing that specimens be collected and be deposited in the museum of the university. In due course, a state charter was issued, and in 1871, as a *quid pro quo* for financial assistance, the society relinquished ownership of the museum to the state. Subsequently, the Illinois Museum of Natural History at Normal was rechristened the Illinois State Laboratory of Natural History. The Director of the State Laboratory, Stephen A. Forbes, who also served as State Entomologist, received a professional appointment to the Illinois Industrial University (subsequently the University of Illinois), where we are today. The Laboratory moved with him, as did the Office of the State Entomologist. The two offices remained separate until 1917, when the General Assembly wisely combined them into the Illinois Natural History Survey. The word "survey" clearly implies census, but Forbes, as first Chief of the Survey, interpreted it as the relationship between living organisms and the environment, a forward-looking ecological concept that has directed the Survey to the present day and continues to set the course for the future.

Clearly, during its long history innumerable persons have made outstanding efforts on behalf of the citizens of Illinois through the medium of the Illinois Natural History Survey. Some have devoted entire professional lives to the Survey. Much of their effort has been obscured by time although a legacy remains in the form of publications, collections, and accumulated data. As a unit of state government subject to the whims of political change, the Survey has drifted through an array of reporting structures, most of which were not especially helpful in furthering its activities. Some of these arrangements were, in fact, hostile.

A major organizational breakthrough was made when the Illinois Department of Energy and Natural Resources was formed. Several governmental units, including the Illinois Natural History Survey, with interrelated interests and goals were assembled under this department.

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Dr. Lorin I. Nevling, Jr., is Director of the Field Museum of Natural History, Chicago, Illinois, and serves as a member of the Board of Natural Resources and Conservation, the governing board of the Illinois Natural History Survey. Dr. Nevling presented this address at the 125th anniversary celebration luncheon.

Perhaps for the first time in its long history, the Survey received positive support from the Director to whom it reported. Former Director Beal and current Director Witte must know that we appreciate their support, financial to the extent possible, but equally important, their active interest in the programs of the Survey. Neither has been passive, and both have insisted on programs based on efficiency and effectiveness. This insistence has caused internal examination and, in some instances, the development of new and exciting directions.

The responsibilities of the Survey are founded in law and include:

- to maintain a biological survey;
- to study the biological processes of ecological systems;
- to acquire, organize, and utilize information about the entire fields of entomology, zoology, and botany;
- to recognize needs for, and provide recommendations about, the protection, development, and use of biological resources, including agriculture;
- to publish and furnish information about biological resources and their enjoyment, use, and management according to scientific principles.

Clearly, to respond to such a complex set of activities a diverse, dedicated, *thoroughly* professional staff is required. Today, the staff numbers about 200. The Survey is organized administratively into five scientific research sections so as to respond efficiently to the various demands. These sections are Aquatic Biology, Botany and Plant Pathology, Economic Entomology, Faunistic Surveys and Insect Identification, and Wildlife Research. Laboratory and field facilities are scattered appropriately throughout the state. Each section relies heavily on the collections and accumulated data of the Survey. The collections, *in toto*, number about *6,000,000* items and are the largest and most comprehensive for the state. The larger segments of the collections are:

| | |
|---|---|
| 1. Insects | 4,875,000 |
| 2. Fish | 500,000 |
| 3. Plants | 210,000 |
| 4. A specialized library of bound volumes. | 34,000 |

Specimens do not of themselves constitute a collection – they must be *organized* in some fashion, preserved, and maintained. The Survey's responsibility extends to the use of collections through research.

The term, *research*, can mean a multiplicity of kinds of effort which, for the sake of simplicity, can be thought of in the case of the Survey as being of two nonmutually exclusive types: basic research and applied research. The Survey is actively engaged in both.

When the term, *research*, is used in the scientific community, basic research is almost always implied. Basic research stresses original scholarship, i.e., it adds to the base of human knowledge. Typically, the questions that are to be answered are posed by the individual researcher, and it is this ability which makes the Survey scientist most akin to a university research professor. The Survey makes a heavy investment in basic research because our future problem-solving capability will depend significantly on the bedrock of knowledge provided by basic research.

For example, is it important to maintain a large insect collection and research program? Up to 3,000 animal species, mostly insects, are occasionally or potentially harmful. About once every 3 years, a new insect pest of major importance enters Illinois. Without comprehensive collections and trained personnel, prompt identification would not be possible, and prompt identification *is* one of the keys to effective control. Some of the recent pests which have found Illinois to be a land of opportunity are the western corn rootworm, gypsy moth, crucifer weevil, and a Mexican bean beetle that feeds on soybeans.

Some other basic research programs of the Survey are the floristic and faunistic surveys which have made Illinois one of the biologically best known areas in the world. The Survey's data base is unquestionably the finest of any state. One of the benefits of the Survey's long existence is the opportunity to repeat surveys at intervals and, thus, to monitor changes that have occurred in populations and natural habitats within the state.

Eventually and irreversibly, we will find it necessary to undertake a biological survey of the United States. When that day comes, Illinois will provide the keystone leadership for the nation.

Two examples of the importance of resurveys, both from ornithology, show the value of such activities. Beginning with classical work in 1885, *The Ornithology of Illinois*, published in two volumes in 1889 and 1895, the Survey has produced a series of bird studies unequaled in any other state. In 1906, the Survey began a series of statewide censuses of birds in Illinois. These surveys were repeated 1956–1958 and found about the same number of breeding birds in Illinois. But in 1909, 18 species constituted 70 percent of the breeding birds, whereas in 1957 only 9 species constituted 70 percent. These changes were brought about by habitat changes, and these changes are still occurring rapidly.

Canada geese were first studied by the Survey in 1941, and these studies continue today. As a result, we now understand the condition factors of the birds and their relation to seasonal stress, management techniques, and various diseases and parasites. In 1962, a Survey scientist rediscovered the then-presumed-extinct giant Canada goose and provided the rationale necessary to reestablish this subspecies over much of its former range.

Research on the soil insecticides aldrin and heptachlor conclusively demonstrated that the epoxides of these insecticides are translocated from the soil and are stored in the oil of soybeans and in the oils and waxes of pumpkins. Aldrin and heptachlor were widely used as soil insecticides in the 1950's and 1960's, and the Survey's research has had a tremendous impact nationally and internationally in controlling the unwarranted use of these chemicals.

Other ecological research includes the study of ponds, streams, rivers, and more specialized bodies of water, such as reservoirs and cooling lakes. In specialty areas, there are, for example, studies of fish larvae, genetics, and behavior; insect behavior, including overwintering, migration, and dispersal; as well as insect-host interactions.

Applied research is the application of basic research findings to a problem to develop a resulting product or answer. The questions are usually thrust on, or assigned to, a researcher, and it is the kind of research most often carried on in the corporate world under the title, research and development. As the needs of the people of Illinois drive many research questions, much of the Survey's work is of this nature and encompasses many diverse elements, including:

> Studies carried out under a grant or contract for governmental agencies or business firms when their needs fit Survey interests and expertise. Usually, these studies are designed to answer specific management questions.
>
> Major plant-related activities, including the identification of plants and plant diseases for the public and industry. Two examples are the discovery of the causal agent in brittleroot disease of horseradish and its transmission by the beet leafhopper, and the concept – now well accepted in corn-producing states – that black cutworm larvae that damage young corn plants in the spring come from eggs oviposited on the weeds in a field before the corn is planted.
>
> Effects of soil and air pollutants on plant growth and development and crop yield and quality.
>
> Studies on the prevention and control of diseases of greenhouse plants, woody ornamentals, and

shade trees. Specific problems, such as oak wilt and walnut and sycamore anthracnose, are being addressed.

In zoology some projects are:

Identification services for the public and industry, management plans for fish, aquaculture, or the best use of wildlife resources for the preservation of the prairie chicken.

Development of insect pest management programs by integrating cultural, biological, and chemical controls into crop production systems. A marvelous achievement was the publication of the manual, *Soybean Insect Identification and Management in Illinois.*

Studies of the transmission of diseases and parasites between wild and domestic animals and between wild animals and man.

For years, Survey scientists have carried on interdisciplinary research. This is the end of the rainbow for most research institutions. At the Survey, the rainbow is just down the hall or up the stairs.

A particularly impressive piece of interdisciplinary long-term research is being continued on the Illinois River system. From the first years of its formation, the Survey has worked on this river, relating changes in water quality and river use to changes in the plankton, benthos, and fishes. Diversion of Lake Michigan waters through the system, channelizations with locks and dams for navigation, enrichment by sanitary wastes from Chicago, and draining of the floodplain lakes for agriculture have caused dramatic changes in the aquatic communities. The Survey's investigations of these changes have attracted an impressive array of scientists, have made the Illinois one of the world's best-studied rivers, and recently have gained national support to intensify the investigations for another two decades under the National Science Foundation's Long-term Ecological Research program.

No matter what the nature of the research carried out by the Survey, the results must be made available to the appropriate publics. This publication of results is accomplished in a variety of scholarly journals, books, monographs, brochures, and special reports.

In the last year alone, staff activities have resulted in five books, 17 book chapters, 98 scientific journal articles, 85 project reports, and 94 papers presented at professional meetings.

Newsletters and press releases are sent weekly to newspapers and radio and television stations throughout the crop season to keep the public abreast of developing problems. There are programs and workshops for school children and specialized groups, such as the professional pest consulting industry. *Every* person in the state is touched directly or indirectly by Survey research results, such as recommendations concerning the protection of crops from crop pests, on reducing disease in ornamental plants, and for the management of fish and wildlife populations.

Survey scientists also attend the meetings of, and are active in the affairs of, national and international scientific organizations. In short, the Survey is everywhere and has developed substantial local, national, and international reputations.

Previously, I mentioned the positive step of placing the Survey under the Department of Energy and Natural Resources. We were placed there along with our sister organizations, the Illinois State Water Survey and the Illinois State Geological Survey. A history of cooperative efforts among the three Surveys existed, but cooperative efforts usually were on a scientist-to-scientist rather than Survey-to-Survey basis.

Within recent years, a series of changes in the leadership of the Department and the three Surveys has occurred. The principals were Michael B. Witte, Director; Robert E. Bergstrom, Acting Chief of the Geological Survey; Stanley A. Changnon, Chief of the Water Survey; and Paul G. Risser, Chief of the Natural History Survey.

The chorus was comprised of the members of the Illinois Board of Natural Resources and Conservation. In my opinion, a synergistic reaction has taken place among the parties in such a way that the Surveys are changing more than at any time in their combined histories. Change is a frightening thing to all of us, but we are convinced that the opportunities are unlimited.

Stimulated by Director Witte and the Board, the Surveys presented proposals for interdisciplinary research that were inter-Survey in nature. These proposals were innovative and had far-reaching consequences. Only a few could be funded, but the effort has produced a new spirit of cooperative research among the Surveys.

What are the demands on the Survey likely to be in the future? A few can be predicted. We will:

> Monitor the health of species populations and ecosystems. We will recognize significant changes, separating long-term trends from short-term fluctuations, especially for species population numbers and distribution as well as for ecosystem characteristics, such as primary production and nutrient cycling and retention.
>
> Respond to specific problems as these issues arise, but also maintain a steady basic research program driven by scientific questions.
>
> Draw together diverse disciplines to address, in a coherent fashion, complex topical problems, such as hazardous waste management and wildlife populations in landscapes continually managed by man, and organize information for decision-making that combines ecological with economic considerations.
>
> Develop the ability not only to describe the natural resources of the state, but to predict the consequences of alternate management schemes and possible demographic and energy scenarios.
>
> Provide a central location where one can obtain information about natural resources or receive guidance as to the location of natural-resource data and information.
>
> Maintain a competitive edge in the quality of natural-resource research, not only to solve our problems effectively and manage our resources wisely, but to continue to attract and retain the very best scientific staff.
>
> Finally, we will need to move fully into the computer age so that the incredible data locked into collections can be fully utilized. It seems to me that this will be the only way to maintain open-end excellence with closed-end funding. Our immense data base, if united with those of our sister Surveys of Water and Geology, will form the most potent environmental data base available *anywhere.*

I am certain that Stephen Forbes would be proud of all those, past and present, who have contributed their talents to bring the Illinois Natural History Survey closer to the idea of understanding the relationships among living organisms and the environment. No one can tell what the most important problems of society will eventually turn out to be, but we can be sure that many of them will be tied to a deeper understanding of ourselves and our environment.

# Lake Tahoe: A Microcosm for the Study of Change

Charles R. Goldman

The concept of "The Lake as a Microcosm" was first proposed by Dr. Stephen Alfred Forbes, first Chief of the Illinois Natural History Survey. This work (Forbes 1925), presented before the Peoria, Illinois Scientific Association in 1887, has become a classic among ecologists and is often cited as an example of the interdependence of organisms within a lake. In developing this theme to its maximum, Forbes suggested that the organisms of Illinois lakes were largely independent of their terrestrial surroundings. It can be convincingly argued that in 1887 the plants and animals inhabiting Illinois lakes were in fact a lot more independent of their surroundings than they now are. It is clear, however, from reading his monumental work, *The Fishes of Illinois* (Forbes & Richardson 1908), that he was aware of the sewage pollution from Chicago entering the Illinois River system. Today, man is having a dramatic effect on most of the world's watersheds, which in turn play an increasingly dominant role in establishing the physical characteristics of lakes. These characteristics include color and transparency as well as such biologically mediated factors as fertility and trophic status.

Eighteen years before Forbes' article appeared in the United States, S. A. Forel (1869) was founding the science of limnology at Lausanne, Switzerland, on the shores of beautiful Lake Geneva. His brilliant treatise, *Monographie Limnologique*, provided a bench mark for the study of the drastic changes that were to alter this lake as well as the Lake of Zurich during the century to follow (Forel 1892, 1895). Immediately following the 1983 International Congress of Limnology in Lyon, France, an entire week was devoted to assessing the status of Lake Geneva and attempting to develop a strategy to bring nutrient loading from both Swiss and French sources under control (Fig. 1). Perhaps by coincidence or as a result of scientific information exchange, John Le Conte (1883a, b, 1884) measured the transparency of Lake Tahoe near the crest of the Sierra Nevada in 1873. Le Conte's observations of Lake Tahoe appeared in a regional stagecoach journal, *The Overland Monthly.* Lake Tahoe, bordered by two states rather than two countries, has been successful in achieving total sewage diversion from its basin, yet continues to decline in water quality from an array of nonpoint nutrient sources (Fig. 2).

Disturbance of the Tahoe basin has been very recent in the geologic sense of time. The first major perturbation occurred about 1846 when most of the mountainsides surrounding the lake were cleared of virgin timber to be used for shoring up the mines of the Comstock in Nevada. The second disturbance came during the years immediately followng World War II after new growth had reestablished the forest. This period was marked by rapid human population growth (Fig. 3) and a great deal of road and housing construction. Despite the efforts of conservation groups and state and federal agencies to regulate development, growth continues to this day. As the tourist and resident population of the basin increased, from about 10,000 in 1955 to nearly 80,000 in 1979, real estate prices rose rapidly, and the year-round use of the basin has continued to increase. With this growth, the

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Fig. 1. – Lake Geneva, nestled in the Alps, is bordered by both Switzerland and France. It has suffered from heavy nutrient loading from both countries for more than a century. Photo by the author.

Fig. 2. – Looking southeast across Lake Tahoe from 19,000 feet (5,800 m). The enormous volume of the lake has served to buffer the nutrient input from its disturbed watershed. Still, the primary productivity has increased at the rate of 6.3 percent per year. Photo by Robert C. Richards.

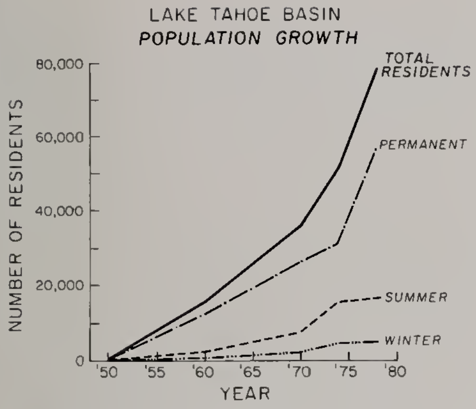

Fig. 3. – Population growth in the Lake Tahoe basin from about 1950 through 1977. The population has been divided into winter, summer, and permanent residents. The sum of both seasonal and year-round residents is presented as total residents.

deterioration of Lake Tahoe, like that of many of the world's lakes, has accelerated. This paper continues the documentation of the changing lake and attempts to isolate some of the major factors involved. Through a better understanding of whole-system response, it should be possible to make more intelligent management decisions and eventually stabilize the fertility of lakes at some acceptable level.

## EUTROPHICATION OF LAKES

Naumann (1919) used the concept of trophic status to distinguish between the oligotrophic mountain lakes and the more productive eutrophic lakes of the lowlands. Many of the world's lakes, like Tahoe, have experienced a steady increase in fertility as their watersheds have been developed for agriculture, silviculture, or urban communities. Documentation of the change has often included a variety of chemical measures of fertility, such as nitrogen and phosphorus concentrations, changes in the species composition and abundance of algae, and decreases in hypolimnetic oxygen concentration during stratification. Observations of oxygen depletion under winter ice cover or following algal blooms were first made possible by the well-known Winkler technique for measuring dissolved oxygen. The measurement of primary productivity has provided a highly sensitive integration of chemical, physical, and biological conditions in lakes (Goldman 1963; Goldman & Wetzel 1963). Comparison of the contrasting vertical profiles of *in situ* measures of primary productivity from lakes of different trophic status has previously been presented (Goldman 1968). These profiles show how the euphotic zone is compressed as algal growth shades out the deeper water.

Perhaps the most publicized example of eutrophication in North America has been Lake Erie, which, during the last several decades, has undergone a dramatic increase in fertility and general deterioration in water quality. This eutrophication resulted from a combination of urban and agricultural discharge and caused serious seasonal oxygen depletion in much of the lake. Efforts to reduce nutrient loading appear to be meeting with success, and improved conditions have been reported in recent years. Because water levels have also been higher than average in the Great Lakes in recent years, simple flushing of the system may also be a factor in their improvement. It will be important to follow their trophic status through different hydrologic conditions in the years ahead.

In addition to Erie, others of the Great Lakes have also increased in fertility, with a concomitant change in the fisheries (Beeton 1969). The invasion of the sea lamprey and alewife had dramatic effects on Great Lakes fisheries, but industrial and domestic pollution also have caused great concern. Despite continuing public and governmental agency concern about heavy metals and industrial organics accumulating in fisheries products, there is a general impression that control measures are currently returning high dividends for the investments in pollution control and fisheries management. There remains, however, the need for cautious concern. Although increased fertility doubtlessly provides the potential for an increase in the standing crop of fishes, large populations of exotic predatory salmon may begin to exert a negative impact on their food resources. The alewife population, in particular, has undergone dramatic reductions, and other fishes may be subject to similar predation. Further, the large reduction in alewives may be expected to have influenced zooplankton populations.

Perhaps the first example of eutrophication (Ruttner 1963) was the Zurichsee in Switzerland, which became eutrophic in 1896 and showed a difference in fertility between its upper and the lower basins. In what was probably the first attempt at lake restoration, sewage treatment was initiated and has been credited with greatly improving the condition of this lake.

Another large Swiss lake, the Bielersee, became eutrophic following the diversion of the river Aare into the lake and the concomitant increase in nutrient loadings after 1930 (Tschumi et al. 1982). Despite phosphorus reductions of more than 50 percent, Bielersee has shown little improvement. Nitrogen loading remains high from a drainage area that has been increased by 2.6 times. It is apparent that the phosphorus levels are still sufficient to sustain eutrophic conditions at the current level of nitrogen input.

Even Siberia's Lake Baikal, the world's oldest and deepest freshwater body, has not been immune to the impact of man's activities (Fig. 4). The harvest of the slowly growing, mixed deciduous and coniferous forests along its shores and the discharge from a large cellulose plant and other industries along the Selenga River were responsible for catalyzing what was certainly the most publicized, if not the first, environmental movement in the Soviet Union. Fortunately, the lake's enormous volume (23,000 km³) provides

Fig. 4. – Lake Baikal, USSR, is the oldest and deepest lake in the world. Despite its enormous volume, it has been subject to pollution from forest cutting and industrial development. The 500-ton limnological research vessel *Vereschagin* lies at anchor. Photo by the author.

tremendous dilution of pollutants (Goldman 1973). The largest lake in Europe, Ladoga, near Leningrad, is also subject to pulp mill pollution as well as other industrial contamination, and progressive eutrophication has been reported.

Although many of the world's major lakes have experienced varying degrees of eutrophication, detailed studies of change at various levels of the food chain have usually been lacking. One long-term data set developed by Lund (1964), which featured the annual silicon depletion cycle of diatoms in Lake Windermere, England, is noteworthy although the lake does not appear to have changed much during the 16-year record.

The public is usually first alerted to pollution by the appearance of dead fish along the shore or by the development of large blooms of blue-green algae, which can give a once-blue lake the green appearance of a lawn. An unusually warm summer, drought, or the application of commercial fertilizers to the watershed may trigger a severe algal bloom and sudden public awareness that a problem exists. It is likely, however, that the problem of excessive nutrients has been developing over a considerable time. When the change occurs over many years, only the keenest observers notice it, and without long-term collection of good data, change is difficult or impossible to prove.

In the western United States the most detailed studies of the progress of eutrophication have been done for Lake Washington by Professor W. T. Edmondson and for the earliest stages of change in Lake Tahoe, by the author. The Lake Washington studies used measures of chlorophyll *a* concentration as evidence for the increasing fertility of the system, while the Tahoe studies measure the change in the rate of photosynthesis over time.

Concentrations of chlorophyll *a* in Lake Washington increased steadily with the algal concentration as sewage loading increased between 1950 and 1963. The blue-green alga, *Oscillatoria rubescens* de Candolle, became the dominant form in Lake Washington, as it had in Lake Zurich a century earlier. With the collection of sewage from around the lake perimeter and its diversion to Puget Sound, beginning in 1963, transparency returned as chlorophyll values gradually declined during the next decade (Edmondson 1972a, b). With the exception of these last two studies and a long series of fisheries records and chemical measurements from the Great Lakes, there is, in general, a lack of long-term data sets on the limnological changes that have occurred in North American lakes experiencing eutrophication. The value of long-term studies in better understanding how aquatic ecosystems function is now becoming generally recognized (Goldman & Horne 1983; Likens 1983; Goldman & de Amezaga in press). The Lake Tahoe data set is the basis for the following analysis of the first stages of eutrophication in an ultraoligotrophic lake.

## LAKE TAHOE

Lake Tahoe was known only to the Paiute Indians until its discovery by General Fremont in 1844. Mark Twain in *Roughing It* described Lake Tahoe as "surely the fairest sight the whole world affords" and marveled at its clarity. In addition to Mark Twain's observations and the historical records on the Tahoe fishery, probably the most important single data point was that of transparency obtained by John Le Conte in September 1873. Without this simple measure of water clarity, taken with an ordinary white dinner plate serving as a Secchi disc, there would have been endless dispute as to the transparency of Lake Tahoe before development began in earnest.

The lake is the tenth deepest in the world (505 m) and is uniquely situated for study of the early stages of eutrophication. This ultraoligotrophic lake has a small (800 km²) watershed for a lake with 500 km² of surface area. Its enormous volume of 156 km³, with a retention time of about 700 years, provides a large buffering effect for nutrients entering the lake from tributary streams draining the forests, roads, parking lots, golf courses, and building sites of its highly disturbed watershed. Due to the long residence time of the water most of the nutrients entering the lake remain there with little flushing action and only slow sedimentation to reduce them. In addition to stream-borne nutrients and sediment, air pollution is now visible, and storms bring acid rain to the basin as well as an important, but as yet inadequately measured, dry fallout (Fig. 5).

Located at the crest of the Sierra Nevada, Lake Tahoe was first recognized as a graben fault basin by Le Conte (1875). It was probably formed during the upthrust of the mountain range between 3 and 9 million years ago and has a morphometry similar to that of a giant bathtub. The 450-m contour line of depth is very close to shore around most of its perimeter. Important to the lake's trophic status is its relatively infertile watershed consisting largely of decomposed granite derived from the great Sierra Nevada batholith as well as some Precretaceous metamorphic rocks, Pliocene volcanics, and a few cinder cones from the Holocene (Hyne et al. 1972). Ice damming of the Truckee River outlet of the lake occurred during the last period of Pleistocene alpine glaciation. At that time the water in the lake reached levels as much as 150 m higher than it is today.

Because of Lake Tahoe's extremely low productivity, which, since 1959, has ranged from 0.12 to 0.26 g C m$^{-2}$ day$^{-1}$, the more conventional measures of fertility, such as oxygen depletion, chlorophyll *a*, and change in chemical composition, have had little meaning. Oxygen levels have remained at or near saturation all the way to the bottom of the deepest part of the lake

Fig. 5. – Air pollution is now frequently visible in the Tahoe basin during inversions. The smog layer is visible from Rubicon Point on the west side to Tahoe Keys at the south end. Photo by Robert C. Richards, February 1976.

(505 m), and there has been no detectable trend in the nutrient content of the surface waters from year to year. The increased nutrient loading has been so diluted and so quickly incorporated into algal growth that annual increases in such important inorganic nutrients as nitrogen and phosphorus have not been detectable. However, a depletion of nitrate has been found in the surface waters during the main growing season, resulting in a distinct "nitra cline" (Paerl et al. 1975). Following the pattern of vertical stratification of nitrate through the following fall and winter gave the first proof that waters in Tahoe actually mixed all the way to the bottom. However, for practical purposes this mixing occurs only during particularly stormy, cold winters. Deep mixing can provide a greatly elevated nitrogen concentration for the spring growing season and is an important factor in determining year-to-year variations in productivity. When mixing occurs, internal nutrient loading from this deep nutrient storage is likely to be reinforced by runoff from the very storms that cause the mixing. The deep waters of the lake provide a large reserve of nitrate during years when winter mixing is incomplete (Goldman 1981).

My data collection for Lake Tahoe began in 1958 and 1959 with the first measurements of primary productivity, using the sensitive carbon-14 method (Steemann-Nielsen 1952) with the modification of Goldman (1963). Transparency and an array of other limnological measures were also included as well as extensive bioassays of nutrient-limiting factors (Goldman 1964, 1981; Goldman & Armstrong 1969; Arneson 1979). Intensive sampling began in 1967 and has continued to this time. The measurement of primary productivity provides a sensitive integration of the physical, chemical, and biological factors controlling photosynthesis by the free-floating phytoplankton component of this low-fertility environment. In addition, the data have enabled us to show significant change long before conventional methods would have detected it. The primary productivity of the lake has more than doubled in a 20-year period at an average rate of increase of over 6 percent per year (Fig. 6).

Peak years of productivity in this progression took place in 1975 and 1980. After those years of particularly high primary productivity, there followed 2 consecutive years of lowered productivity. If only a single lake had been studied, one might easily and erroneously have concluded that weather or changing meteorological conditions, such as were caused by El Niño (Strub et al. in press) in the western United States, were responsible. But data collection using exactly the same technology had been started at another subalpine lake, Castle Lake, in 1959 and has continued without interruption for 25 years. This small (50 ha) lake, like Tahoe, has a very small watershed relative to its surface area and shows nitrogen limitation. No upward trend in productivity is evident in this lake (Goldman & de Amezaga in press). In attempting to correlate the precipita-

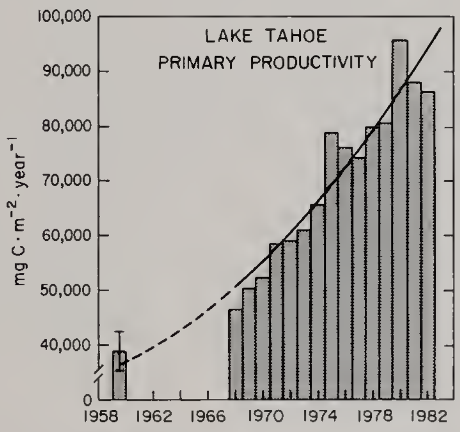

Fig. 6. – Annual primary productivity in Lake Tahoe, California-Nevada, between 1958 and 1982. Each year represents the integration of weekly or biweekly measurements made using the Carbon-14 method at a series of depths extending from the lake surface to 105 m. Approximately 35 sampling dates for each year are represented in this figure. The curve represents a least-squares fit over this time span.

tion at Lake Tahoe with the annual primary productivity, we discovered that there was no correlation if a direct regression was run. However, if we plotted the percentage of change from the previous year's productivity, a positive relationship emerged (Fig. 7). This finding suggests that the lake's "memory" of the previous year's productivity is more important in establishing the positive relationship with rainfall than is the irregular but upward trend in fertility evidenced by the productivity curve (Fig. 6).

The relationship between rainfall and primary productivity in Lake Tahoe, however, is somewhat more complicated than this explanation implies. Not only does rainfall influence the annual nutrient input to the system, but it is also related to storms which cause internal nutrient loading of the euphotic zone and deep mixing of the nitrogen-enriched hypolimnion of the lake. Further, a rainy year, because of increased cloud cover, causes a reduction in solar radiation and in temperature. In 1982, for example, high rainfall as a result of El Nino was accompanied by one of the darkest years on record at Lake Tahoe (Fig. 8). This darkness may have decreased the expected productivity from nutrient runoff and contributed to the reduction of the average depth of the euphotic zone from the previous year by almost 2 m (Fig. 9). Therefore, 1982 did not fit the regression of more typical years. The high nutrient levels from the heavy runoff in 1982 coupled with deep mixing enabled the phytoplankton to use the decreased available light more efficiently in both Castle Lake and Lake Tahoe than they had in the previous year (Goldman & de Amezaga in press).

Another evidence of the value of long-term data collection was apparent when it was discovered that the two cladoceran members of the endemic zooplankton population, *Daphnia* and *Bosmina*, had disappeared from the lake. The opossum shrimp, *Mysis relicta* loven, introduced as a food for the resident lake and rainbow trout populations as well as for the Kokanee salmon, emerged as the major suspect in the ensuing investigation (Richards et al. 1975; Goldman et al. 1979). Following a crash in the *Mysis* population, first *Bosmina* and then *Daphnia* have made weak but promising returns to the plankton of the lake (Fig. 10). Observations of other western lake systems indicate that *Mysis* will coexist

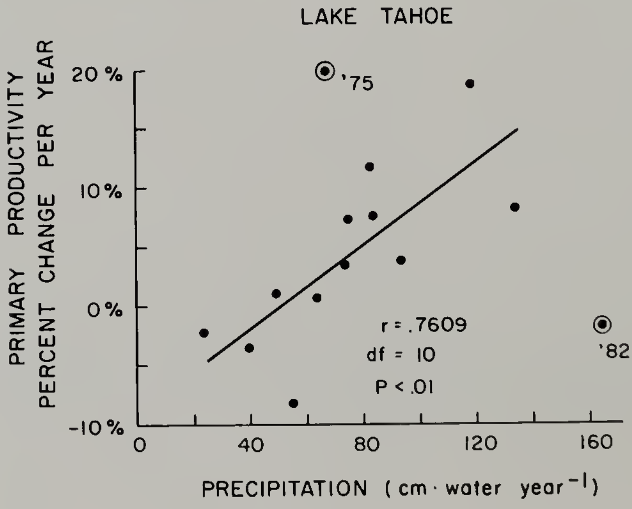

Fig. 7. – Percentage change in annual (1 January–31 December) primary productivity in Lake Tahoe is regressed on total precipitation for the corresponding "water year" (1 October–30 September) for the period 1969–1982. Two unusual years, 1975 and 1982, have been excluded from the regression. (From Goldman & de Amezaga in press).

with cladocerans if the fertility level is appreciably higher than Tahoe's and if warm water provides thermal refuges for the cladocerans.

One way to extend the information time series for any lake study is to examine lake sediments. Lakes are, after all, reservoirs of history in the sense that they usually store in their sedimentary records evidence of the events that have occurred on their watersheds. Erosional deposition from the building

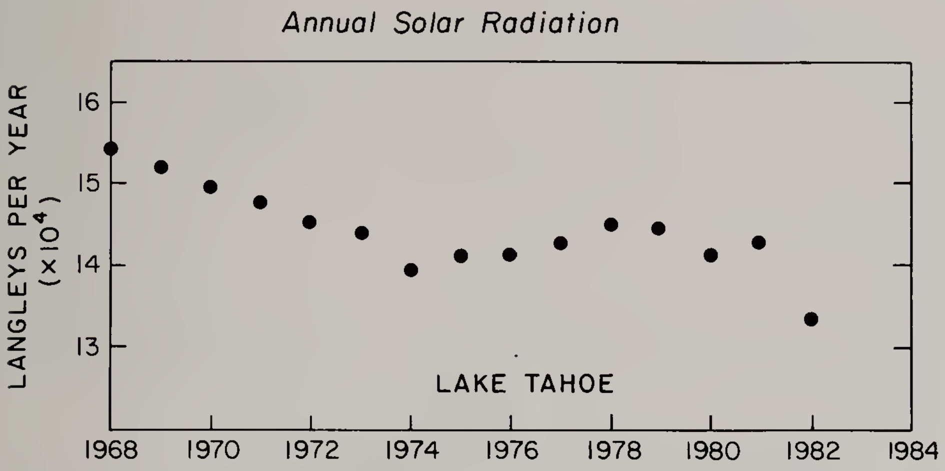

Fig. 8. – Annual solar radiation measured at Lake Tahoe, California-Nevada, between 1968 and 1982. Daily light curves made with a continuously recording pyrheliometer were digitized and summed to obtain the total solar radiation for the year in langleys.

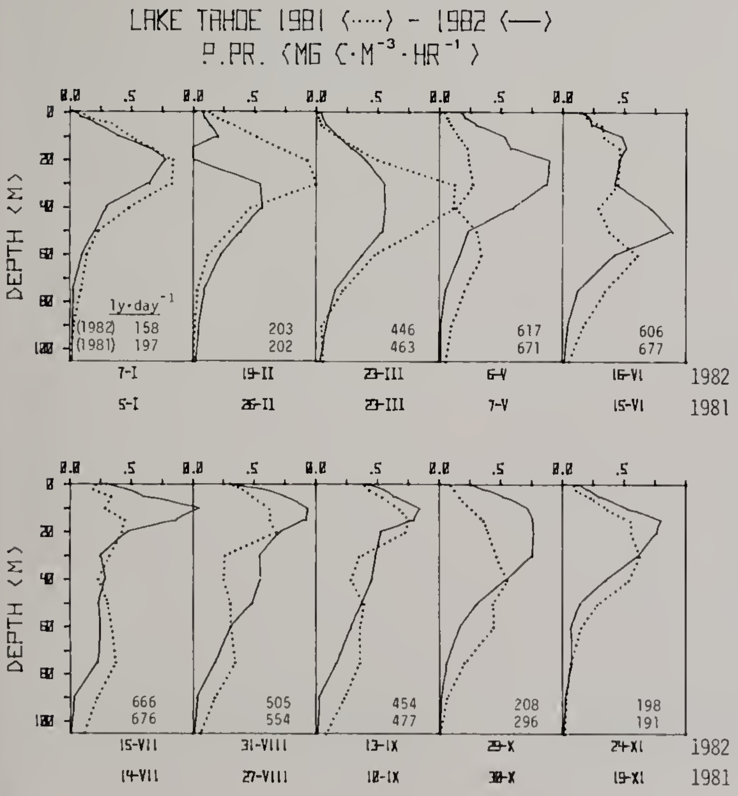

Fig. 9. – Vertical profiles of primary productivity taken *in situ* in Lake Tahoe in 1981 and 1982. The peak of production was higher in the water column during the cloudy, high-precipitation year 1982 as compared with 1981, which was clearer and drier. The solar radiation available on each day is shown at the bottom of each vertical profile. The rather consistently higher solar radiation in 1981 is evident.

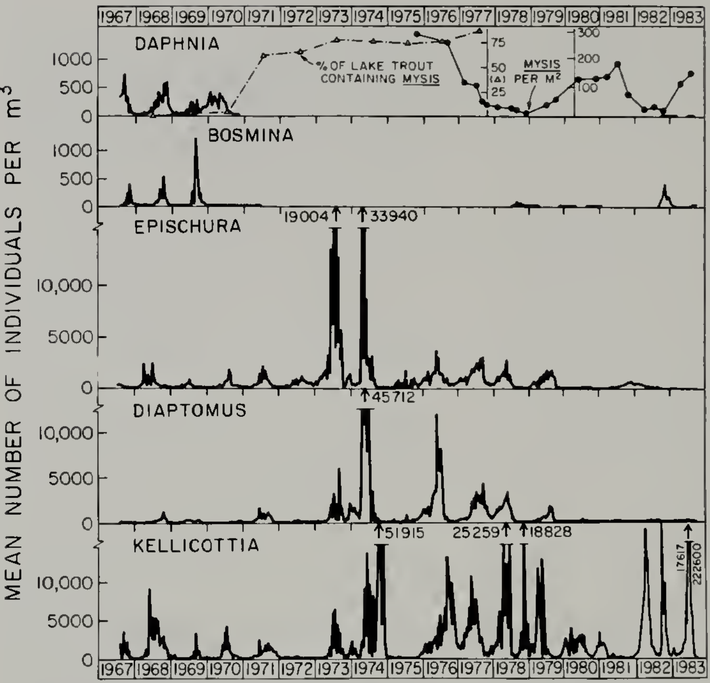

Fig. 10 – Variations in populations of *Daphnia, Mysis, Bosmina, Epischura, Diaptomus,* and *Kellicottia* in Lake Tahoe between 1967 and 1983. *Mysis* values from the years 1968 to 1977 are based on the percentages of lake trout containing *Mysis* during creel censuses by the California Department of Fish and Game. Beginning in 1975, *Mysis* values were determined on the basis of a lakewide average (data through 1980 from Goldman [1981]).

of the Roman road, Via Cassia, about 2,000 years ago is evident from a sediment core (Cowgill & Hutchinson 1970). Sediment from erosion, ash from volcanic eruptions, as well as that portion of the biota which is resistant to decay may lie undisturbed in sediments for thousands of years. Further, pigments (Vallentyne 1960) and evidence of water chemistry may also be retained in the paleolimnological record.

One of the arguments presented for the continued development of the Tahoe basin was that the lumbering activities of the 1860's did not appear to have done serious damage to the water quality of Lake Tahoe. By examining sediments, we were able to demonstrate that damage done during the initial removal of timber from the basin was small in comparison to the disturbance that has accompanied modern developments. Samples taken in midlake with a large box-coring device clearly show that much more nitrogen is now entering the lake relative to carbon (Fig. 11A). Fig. 11B shows the carbon content of nearshore sediments in the vicinity of extensive lumbering activity during the 1860's. Although there are insufficient lead dates to confirm the 1860 level, it is indicated by estimated sedimentation rates. Similarly, the input of another important algal nutrient, iron, has greatly increased with erosion from the steep slopes of the basin (Fig. 12). In addition, the diatom composition has shifted from centric forms to increasing numbers of pennates (Fig. 13). Finally, Pb-210 dating of the sediments indicates a more rapid rate of accumulation during the last several decades than occurred during the period of forest cutting in the 1860's (Byron & Goldman 1984).

As we look back in time, so must we look forward. The future of Lake Tahoe can be predicted with increasing certainty as the years of data are added, one to another. What seemed to some to be speculation or doomsmanship in the 1960's has been transformed into highly significant regressions. Further, visible periphyton growth now covers the once clean littoral zone so that, in spring, any observer can see a green margin around Tahoe (Fig. 14). Primary productivity correlates significantly

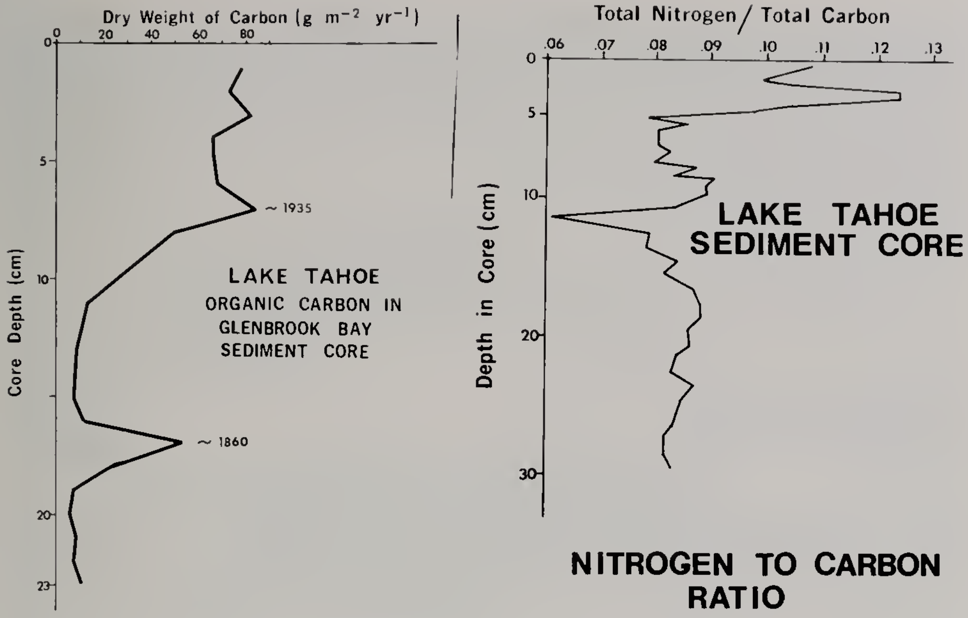

Fig. 11. – (A) The dramatic increase in nitrogen deposited as sediment in Lake Tahoe is evident from a midlake core sample. The higher nitrogen-to-carbon ratio in recent years is obvious (Byron & Goldman unpublished). (B) High organic carbon input is evident from this nearshore sediment core collected in Glenbrook Bay. This area was subjected to extensive timber clearing during the 1860's. Both charcoal and sawdust are to be found in the sediments here.

at the 1-percent level with the decline in transparency and, if projected into the future, predicts a lake of very ordinary transparency within about 40 years (Fig. 15). With each year that the productivity continues its rise, the

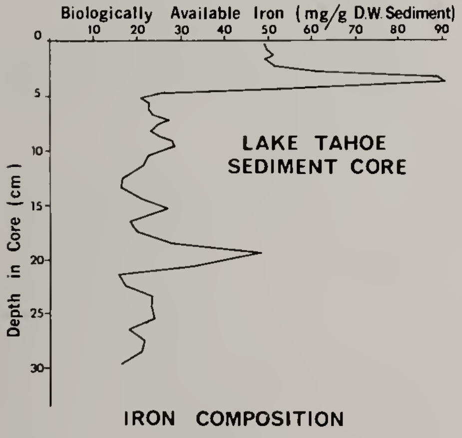

Fig. 12. – Distribution of biologically available iron in a midlake core sample from Lake Tahoe. The rise at 20 cm probably represents the 1860 lumber removal, and the increase above 5 cm is probably due to recent development in the basin (Byron & Goldman unpublished).

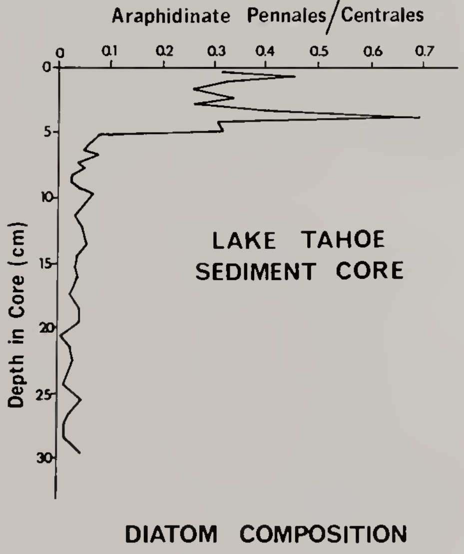

Fig. 13. – The ratio of araphidinate pennate to centric diatoms versus depth within a Lake Tahoe sediment core (Byron & Eloranta in press).

Fig. 14. – Periphyton covers the littoral zone of Lake Tahoe during the spring months. This underwater photograph was taken near Sunnyside (northwest Tahoe) on 8 May 1982 at a depth of 4 m. When this growth breaks loose, it coats the beaches with a brown slime. Photo by Stanford Loeb.

regression line steepens and the number of future years with clear waters in "the lake in the sky" is reduced. The damaged watersheds must be repaired now through the application of innovative biological engineering and further development must be more strictly regulated. Otherwise, future generations will look back and wonder why, with so much knowledge and technology available, we failed to preserve the quality of this remarkable lake microcosm whose exceptional transparency became a legend.

## ACKNOWLEDGMENTS

This work, done over a period of 25 years, would not have been possible

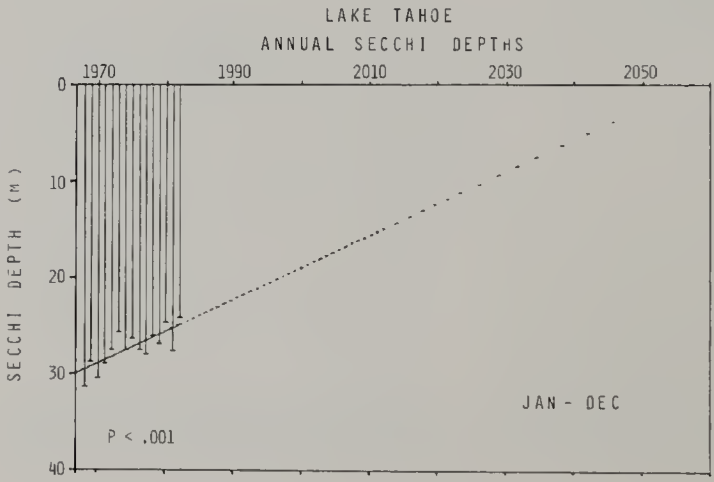

Fig. 15. – The regression constructed from the average annual Secchi depth in Lake Tahoe from 1968 through 1982. The regression line as extended is admittedly futuristic as it extends to a theoretical zero point, which occurs sometime after the middle of the next century. With each additional data point, the regression line steepens and the degree of steepness provides some insight into alternative futures.

without the tireless efforts of the Tahoe Research Group. Robert C. Richards has been particularly invaluable in the collection of data during the last 17 years of this effort and has provided valuable photographic documentation. Data reduction and figure preparation were largely accomplished by Patricia Arneson and Evelyne de Amezaga. Word processing of the manuscript was kindly provided by Carol Barnes, Anne C. Forcella, and Meryllene Smith. George Malyj provided important assistance with various aspects of coordination.

This paper is dedicated to the memory of my father, Marcus Selden Goldman (1894-1984), who first interested me in the streams and lakes of Illinois and, for more than 50 years, enthusiastically endorsed the varied activities of the Illinois Natural History Survey. He was a close friend of many of its staff, an enthusiastic amateur ichthyologist (Goldman 1977), a life member of the Izaak Walton League of America, and a staunch supporter of conservation activities everywhere.

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# A Comparison of the Embryonic Development of Northern, Florida, and Reciprocal $F_1$ Hybrid Largemouth Bass in Different Thermal Environments

David P. Philipp, Christine Kaminski, and G. S. Whitt

The two subspecies of largemouth bass, *Micropterus salmoides salmoides* and *M. s. floridanus*, naturally occur in different geographic and climatic regions of the United States, with hybrids occurring in a zone of intergradation between these regions. Genetic differences between these stocks are reflected by differing physiological responses to the thermal environment. To determine the extent to which these differences contribute to natural geographic separation of the subspecies, we produced the embryos of the four genetic stocks of largemouth bass (*M. s. salmoides, M. s. floridanus, M. s. salmoides* ♀ × *M. s. floridanus* ♂, and *M. s. floridanus* ♀ × *M. s. salmoides* ♂) in vitro, using artificial fertilization techniques. The developmental success of the embryos and the schedule of embryogenesis for each stock were compared at each of a series of temperatures. The developmental success of each stock at each incubation temperature was determined by total hatching percentage. In addition, the thermal requirements for embryonic development of each of these four stocks were compared by determining the $\alpha$-threshold temperatures of development as well as the number of thermal developmental units required to reach each of 22 key embryonic stages. Significant differences in the thermal requirements for embryogenesis exist among these different stocks of largemouth bass. The implications of these findings on current and future largemouth bass management programs are discussed.

The morphological differences between the northern largemouth bass, *Micropterus salmoides salmoides* (Lacepède), and the Florida largemouth bass, *M. s. floridanus* (Le Sueur), were discussed by Bailey & Hubbs in 1949. Since that time a number of studies designed to further assess the differences between the subspecies have been conducted (Hart 1952; Clugston 1964; Addison & Spencer 1972; Zolczynski & Davies 1976; Inman et al. 1977; Cichra et al. 1981; Smith & Wilson 1981; and Wright & Wigtil 1981). These studies have shown that a variety of biological differences exist between these two subspecies.

Our recent electrophoretic survey of the genetic structure of largemouth bass populations in the United States (Philipp et al. 1981, 1982, 1983) has quantified the degree of genetic divergence between these two subspecies. We have described a fast and reliable means of identifying pure northern, pure Florida, or intergrade populations of largemouth bass, that of the electrophoretic determination of the allele frequencies at the Idh-B and Aat-B loci. Meristic and morphometric counts routinely used in the past by fisheries biologists to distinguish these types of populations (Bryan 1969; Addison & Spencer 1972; Buchanan 1973; Inman

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et al. 1977; Moyle & Holzhauser 1978; and Bottroff & Lembeck 1978) are ambiguous and, hence, unreliable. In at least one study (Pelzman 1980) electrophoretic techniques also proved unreliable, since analyses were inappropriate and data were misinterpreted.

Our biochemical genetic analyses of largemouth bass populations (Philipp et al. 1981, 1982, 1983) also demonstrate that the intergrade zone between the ranges of the two pure subspecies, as it exists today (northern Florida, Mississippi, Alabama, Georgia, South Carolina, North Carolina, Virginia, and Maryland), is much more extensive than that described by Bailey & Hubbs (1949). As a result, the previously assigned genetic status of the stocks of largemouth bass used as representatives of the two pure subspecies in many previous studies appears questionable. In the absence of genetic confirmation of the stocks used, the data generated by these earlier studies and their resulting conclusions must be considered very cautiously.

In 1959, Florida largemouth bass, or at least largemouth bass containing some portion of the genome of *M. s. floridanus*, were introduced into certain waters in California (Sasaki 1961). The subsequent establishment of largemouth bass populations with a substantial proportion of the gene pool contributed by the Florida subspecies has been well documented (Smith 1971; von Geldern & Mitchell 1975; Bottroff & Lembeck 1978; Moyle & Holzhauser 1978). The populations of largemouth bass which existed in California prior to 1959 were the result of introductions of northern largemouth bass imported from Illinois in 1891 (Shebley 1917) and were not the result of immigration and natural selection, since the state of California is well outside the native range of largemouth bass (MacCrimmon & Robbins 1975). It is not surprising that the introductions of largemouth bass from Florida were successful in southern California, since the climatic conditions more closely resemble those of Florida than of Illinois.

The apparent success of the recent introductions of *M. s. floridanus* in southern California waters and the demand from fishermen for more and larger largemouth bass have apparently provided the impetus for a number of states to initiate Florida largemouth bass programs. These programs range from controlled research with limited introductions to large-scale propagation and widespread stockings. Unlike California, many of these states already contained populations of naturally established largemouth bass. Due to the lack of reliable, quantitative data concerning the genetic differences of the native and introduced stocks and the relative fitnesses of these stocks in different environments, the long-term effects of these introductions upon the existing largemouth bass fisheries cannot be accurately predicted at this time. However, the impact of these stocking programs on the genetic integrity of the native largemouth bass populations in these states could be catastrophic. We have postulated (Philipp et al. 1981, 1982, 1983) that when alleles present in the Florida subspecies are introduced into a population of the northern subspecies, the unique genic combinations initially present may become irreversibly altered. In addition, some of the Florida alleles are likely to be less fit for these new environments. Although the resulting populations may be genetically sufficient in terms of short-term survival, the long-term effect of this genetic mixture would be a lowering of fitness in the recipient population. For these reasons, we have recommended that programs designed to introduce the Florida subspecies into states outside of peninsular Florida but within the native range of the largemouth bass be halted until appropriate research has determined the effects on the recipient populations.

Factors which affect year-class strength among largemouth bass populations are complex. It has been suggested that spawns hatched early in a given year may suffer substantially less mortality than those hatched later in the season (Aggus & Elliot 1975). Therefore, in mixed populations, differential thermal effects upon the reproductive behavior and the rate and success of development between northern and Florida largemouth bass embryos may play a crucial role in determining the relative contribution of each stock to the total year-class production. The current study was designed to assess thermal effects upon the rate and success of the development of embryos of geneticaly defined stocks of both pure subspecies, *M. s. salmoides* and *M. s. floridanus*, and of both reciprocal $F_1$ hybrids.

## MATERIALS AND METHODS

### Parental Stocks

Northern largemouth bass were collected from Clinton Lake, Illinois. Electrophoretic analyses of individuals from this population showed the frequency of the northern Idh-B allele (Idh-$B^1$) and the sum of the northern Aat-B alleles (Aat-$B^1$ and Aat-$B^2$) both to be 1.000, confirming that this population consisted of pure *M. s. salmoides* (Philipp et al. 1981, 1982, 1983). Florida largemouth bass were collected from Lake Dora, Florida. Electrophoretic analyses of individuals from this population showed the frequency of the Florida Idh-B allele (Idh-$B^3$) and the sum of the Florida Aat-B alleles (Aat-$B^3$ and Aat-$B^4$) both to be 1.000, confirming that this population consisted of pure *M. s. floridanus* (Philipp et al. 1981, 1982, 1983). Adult males and females from only these two genetically confirmed populations were used as brood stock throughout this study.

### Production of Embryos

Florida largemouth bass (FLMB) and Florida ♀ × northern ♂ $F_1$ hybrid largemouth bass (F × N) embryos were produced at the Florida Game and Freshwater Fish Commission, Eustis Fisheries Research Laboratory. Northern largemouth bass (NLMB) males were collected in December 1980 from Clinton Lake, Illinois, and were held indoors at 10°C at the Illinois Natural History Survey (INHS). On 2 February 1981, these fish were marked with a right pectoral clip, transported to Florida, and allowed to reach reproductive readiness in outdoor earthern ponds at the Richloam State Fish Hatchery. During February 1981 ripe male NLMB, retrieved from the hatchery, and ripe male FLMB, collected from Lake Dora by electrofishing, were brought to the Eustis laboratory, where they were held in indoor flow-through raceways. On 21 and 26 February 1981, mature, ripe female FLMB were collected from Lake Dora, Florida, by electrofishing and were brought to the Eustis laboratory. The eggs from individual FLMB females were manually stripped into a bowl, mixed, and split into two aliquots in separate petri dishes. One aliquot was fertilized with sperm from a single FLMB male and the other with sperm from a single NLMB male, using methods described in Childers (1967) and Philipp et al. (1979).

Northern largemouth bass (NLMB) and northern ♀ × Florida ♂ $F_1$ hybrid largemouth bass (N × F) embryos were produced in essentially the same manner, with the following exceptions. FLMB males, collected from Lake Dora in February 1981, were marked with a left pectoral clip and were air shipped to the Illinois Natural History Survey to be held indoors at 10°C until they were stocked outdoors in INHS earthen ponds on 10 March 1982 and were allowed to reach reproductive readiness. During May 1981, FLMB males retrieved from INHS ponds and NLMB males collected from Clinton Lake by electrofishing were brought to the INHS laboratory and held indoors. On 13, 22, and 28 May, mature, ripe NLMB females were collected from Clinton Lake by electrofishing and were brought to the INHS laboratory. NLMB and N × F embryos were produced in the laboratory, using the procedures described previously for producing FLMB and F × N embryos.

## Rearing of Embryos

Procedures and equipment used for rearing the FLMB and F × N embryos were identical to those used for rearing the NLMB and N × F embryos. The very dense egg-sperm mixtures, produced as has been described, were allowed to stand in minimal water for 5 minutes to allow for completion of the fertilization process. These newly fertilized eggs were transferred to plastic containers holding about 2–3 cm of water. The eggs were thinly spread within these containers and incubated for 1 hour at 24°C until initial cleavage. For each cross, samples of 100 normally cleaving eggs (2–4 cell stage) were then removed, transferred to each of a number of glass finger bowls containing 24°C water, and allowed to adhere to the glass. The embryos in each finger bowl were acclimated for 1 hour to a specified test temperature, the bowls were covered with nylon netting to allow water circulation but prevent loss of embryos, and the bowls were immersed in an aerated, filtered, 75-liter constant temperature bath at the test temperature. The temperature of each incubation bath was monitored continuously, using dual water temperature probes and a calibrated 12-channel recorder (Chino Works, Ltd., Tokyo, Japan, Model EW 1200).

Morphological development of each set of embryos reared at each temperature was visually monitored, using a dissecting microscope. Prior to retinal pigmentation, each set of embryos was monitored every 2–4 hours. After retinal pigmentatin had progressed, the frequency of visual observation was reduced to every 6–8 hours. The times required to reach each of 22 key morphological stages were recorded for the embryos at each test temperature. Dead eggs or embryos were counted, removed, and recorded at each visual inspection. A photographic record of the morphological development of these embryos was made, using an Olympus JM dissecting microscope with an Olympus photographic attachment and an Olympus OM-2 camera.

## Data Analysis

The success of development was determined by calculating for each set of embryos the percentage of eggs which hatched and of these the proportion which appeared normal.

The $\alpha$-threshold temperature of development, a theoretical thermal value below which embryonic development ceases (Childers 1967), was determined. For each set of embryos raised at each temperature, the time required to reach each of 11 readily identifiable morphological stages was determined, and the cumulative average temperature of development was calculated from the thermal record for each of these stages. For each of the four genetic stocks (NLMB, N × F, F × N, and FLMB) at each developmental stage, average cumulative temperature was plotted versus the inverse of developmental time in hours. The regression equation describing the linear relationship for each of the four stocks was determined from these values (10–12 data points per stage for the FLMB and F × N embryos and 16–18 data points per stage for the NLMB and N × F embryos). The $\times$-intercept determined from each equation is the $\alpha$-threshold temperature determined for that stock, using the values for that developmental stage. The final $\alpha$-threshold temperature for each genetic stock was determined as the average of the values for these 11 stages.

The number of thermal developmental units (TDU) required for an embryo to reach a given stage of development is defined as the number of degree-hours above the $\alpha$-threshold temperature which must be accumulated. TDU values were calculated, using the final value for the $\alpha$-threshold temperature together with the times of development and average cumulative temperatures for each set of embryos of each genetic stock at each of 22 morphological stages of development.

## RESULTS

### Patterns of Development

No qualitative differences in morphogenetic events could be detected among the four genetic stocks of largemouth bass studied (NLMB, N × F, F × N, and FLMB). Therefore, the following morphological features and their developmental sequence hold for the embryogenesis of all four stocks.

The cortical reaction occurs immediately upon fertilization, with the cortical layer becoming raised by 1 minute after fertilization. There follows a confluence of cytoplasm around the zygote nucleus and the resultant formation of the germinal disc. Cleavage is telolecithal, the initial formation of the two-cell stage occurring within 1 hour at 24 °C. Rates of development during the rest of this study depended upon temperature and will be discussed in detail later. Fig. 1A through 1P illustrate the periods of morphogenesis of one set of embryos, FLMB embryos raised at 24.2° ± 0.4 °C. These pictures illustrate the patterns of development for each of the four stocks of largemouth bass embryos studied (NLMB, N × F, F × N, and FLMB). The developmental progression paralleled that described for other centrarchid species (Morgan 1951; Balon 1959; Champion & Whitt 1976; Taubert 1977).

Early cleavage (Fig. 1A) continues, eventually resulting in blastula formation (Fig. 1B). Epiboly commences (Fig. 1C) and progresses through the yolk plug stage (Fig. 1D) prior to the formation of a body axis (Fig. 1E). Embryonic development continues with the formation of increasing numbers of somite pairs (Fig. 1F). The optic cup and pericardial cavity continue to develop. The embryonic heart begins beating, and true circulation with colorless blood starts shortly afterward (Fig. 1G). The tail increases in length, and body contractions increase in number and severity. Red blood cells containing hemoglobin appear just prior to hatching (Fig. 1H). Hatching occurs fairly synchronously for most eggs at normal temperatures (90 percent of the eggs hatched in a 3–4 hour period at 24 °C). The newly hatched embryo is still quite underdeveloped (Fig. 1I), having only limited and unguided movement. After hatching, the heartbeat becomes more vigorous, and the first pigment granules become visible in the retina (Fig. 1J). Pectoral and pelvic fins form as the retina becomes quite darkly pigmented (Fig. 1K). The tapetum lucidum develops, to give the eye at first a silvery and later a golden appearance (Fig. 1L). During this period the rudiments of many of the internal organs, such as the liver, urinary bladder, intestine, and swim bladder, are developing. Following this stage the jaw begins to form (Fig. 1M) and eventually starts to open and close regularly (Fig. 1N), as body pigmentation commences. At this point, the embryos begin to swim off the substrate with increasing regularity (Fig. 1O), eventually reaching a free-swimming stage and active feeding as yolk sac absorption is completed (Fig. 1P). Our monitoring of the development of largemouth bass ceased at this point and did not include an investigation of the subsequent fry and fingerling stages.

### Effect of Temperature on Developmental Success

The percentage of eggs from which embryos (normal and abnormal) hatched was calculated for each set of embryos reared. These results are given in Table 1. The results for the NLMB and FLMB embryos are also compared graphically in Fig. 2. Comparing the two pure subspecies, the FLMB embryos exhibited optimal hatching rates at temperatures (20°–28 °C) substantially higher than those exhibited by the NLMB embryos (17°–24 °C) (Table 1, Fig. 2). These temperature ranges are somewhat lower than the values reported by McCormick & Wegner (1981). In addition, the lower thermal limits for successful hatching were higher for FLMB embryos than for

Fig. 1. – The morphogenesis of largemouth bass embryos. (A) Early cleavage. (B) Blastula. (C) Epiboly-50 percent. (D) Yolk plug. (E) Body axis. (F) Somite development. (G) Heartbeat. (H) Prehatch. (I) Posthatch. (J) Onset of retinal pigmentation. (K) Dark retinal pigmentation. (L) Golden eyes. (M) Jaw formation. (N) Jaw movement. (O) Swim-up. (P) Freely swimming and actively feeding.

NLMB embryos. Conversely, the upper thermal limits for successful hatching were lower for NLMB embryos than for FLMB embryos. Less than 15 percent of hatched embryos appeared morphologically abnormal at each test temperature except for the NLMB and N × F at 30.5°C (100 percent abnormal in each case), the NLMB and N × F at 30.3°C (68.6 percent and 75.0 percent abnormal, respectively), and the FLMB and F × N at 18.5°C (16.3 percent and 18.5 percent abnormal, respectively).

The tendency for both hybrids to exhibit developmental patterns more similar to that of the maternal than that of the paternal subspecies was notable (Table 1). Although the relationship between temperature and hatching percentage for N × F embryos paralleled that for NLMB embryos, the absolute hatching percentage for the N × F embryos was lower than that for the NLMB embryos at most temperatures. The relationship between temperature and hatching percentage for the F × N embryos paralleled that for the FLMB embryos as well. However, the absolute hatching percentage for the F × N embryos was greater than that for the FLMB embryos at most temperature.

## Thermal Limits of Embryogenesis

The $\alpha$-threshold temperature of development were calculated for each of the four stocks of largemouth bass (NLMB, N × F, F × N, and FLMB) using data from each of 11 distinct developmental stages (body axis; 10, 15, 20, and 25 somites; heartbeat; 50-percent hatching; onset of, light, and even retinal pigmentation; and jaw movement). We chose to monitor these 11 stages because they were easily identifiable visually. Because the rates of development for the NLMB and N × F embryos were similar at all of the temperatures studied, the data for these two stocks were combined for $\alpha$-threshold temperature calculations. Data for the FLMB and F × N embryos were similarly combined (Table 2).

The overall $\alpha$-threshold value for each stock was calculated as the average of the values calculated individually from the data for each of the 11 individual developmental stages used (Table 2). The overall $\alpha$-threshold temperature determined for the NLMB and N × F embryos, 12.62 ± 0.27, was significantly higher ($P<0.01$, Wilcoxon's signed-ranks test, Sokal & Rohlf 1973) than that determined for the FLMB and F × N embryos, 11.52 ± 0.77. In addition, the stage-specific $\alpha$-threshold temperatures calculated for the NLMB and N × F embryos were higher than those calculated for the FLMB and F × N embryos at each of the developmental stages used (Table 2).

The upper thermal limits of development can be estimated by extrapolating from the decrease in hatching percentage for a few of the trials at elevated temperatures, >30°C (Table 1). NLMB and N × F embryos did not hatch at temperatures above 30.5°C, and even at temperatures between 30° and 30.5°C there was an extremely high percentage of morphological deformities. These results agree closely with those reported by McCormick & Wegner (1981) for northern largemouth bass embryos. FLMB and F × N embryos, however, successfully hatched at 30.8°C, although at 31.7°C no success-

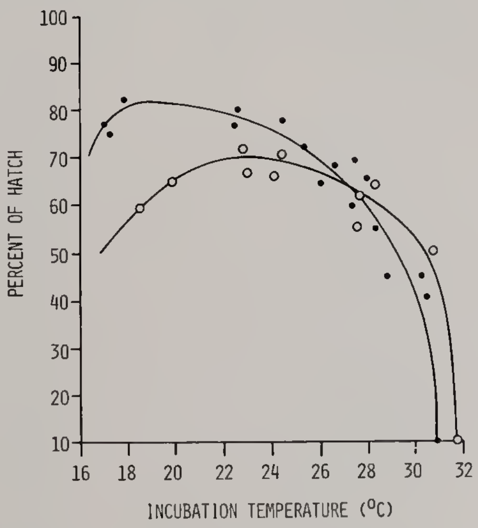

Fig. 2. – The effect of temperature on the hatching success of northern largemouth bass ( ● ) and Florida largemouth bass ( ○ ).

Table 1. — Hatching percentages of largemouth bass eggs incubated at various temperatures

| Largemouth Bass Stocks | | | | | | | |
|---|---|---|---|---|---|---|---|
| NLMB | | N × F | | F × N | | FLMB | |
| Temp (°C) | Percent Hatch | Temp (°C) | Percent Hatch | Temp (°C) | Percent Hatch | Temp (°C) | Percent Hatch |
| 34.0 | 0 | 34.0 | 0 | 36.0 | 0 | 36.0 | 0 |
| 30.9 | 0 | 30.9 | 0 | 31.7 | 0 | 31.7 | 0 |
| 30.5 | 31 | 30.5 | 30 | 30.8 | 47 | 30.8 | 41 |
| 30.3 | 35 | 30.3 | 24 | | | | |
| 28.8 | 35 | 28.8 | 28 | | | | |
| 28.4 | 45 | 28.4 | 37 | 28.4 | 52 | 28.4 | 54 |
| 28.0 | 56 | 28.0 | 53 | | | | |
| 27.5 | 59 | 27.5 | 57 | 27.7 | 63 | 27.7 | 52 |
| 27.4 | 49 | 27.4 | 55 | 27.6 | 54 | 27.6 | 46 |
| 26.6 | 58 | 26.6 | 53 | | | | |
| 26.1 | 54 | 26.1 | 49 | | | | |
| 25.3 | 62 | 25.3 | 55 | 24.5 | 66 | 24.5 | 61 |
| 24.5 | 68 | 24.5 | 61 | 24.2 | 65 | 24.2 | 56 |
| 22.6 | 70 | 22.6 | 66 | 23.0 | 61 | 23.0 | 57 |
| 22.5 | 67 | 22.5 | 64 | 22.8 | 71 | 22.8 | 62 |
| 17.8 | 72 | 17.8 | 60 | 19.8 | 54 | 19.8 | 55 |
| 17.2 | 65 | 17.2 | 61 | 18.5 | 54 | 19.8 | 55 |
| 17.0 | 67 | 17.0 | 62 | | | | |

Table 2. — Alpha-threshold temperatures (°C) of development for the four stocks.

| Developmental Stages | Embryos of NLMB and N × F $F_1$ Hybrid | Regression Equation (Correlation Coefficient) | Embryos of FLMB and F × N $F_1$ Hybrid | Regression Equation (Correlation Coefficient) |
|---|---|---|---|---|
| Body axis formation | 12.17 | $y = 0.00492x - 0.0599$<br>(0.944) | 12.07 | $y = 0.00550x - 0.0664$<br>(0.980) |
| 10 somites | 12.49 | $y = 0.00400x - 0.0499$<br>(0.891) | 10.67 | $y = 0.00394x - 0.0420$<br>(0.975) |
| 15 somites | 12.58 | $y = 0.00358x - 0.0451$<br>(0.905) | 11.10 | $y = 0.00354x - 0.0393$<br>(0.984) |
| 20 somites | 12.79 | $y = 0.00334x - 0.0427$<br>(0.928) | 11.41 | $y = 0.00322x - 0.0367$<br>(0.990) |
| 25 somites | 12.69 | $y = 0.00300x - 0.0380$<br>(0.914) | 12.23 | $y = 0.00314x - 0.0385$<br>(0.990) |
| Initial heartbeat | 12.72 | $y = 0.00272x - 0.0346$<br>(0.926) | 12.22 | $y = 0.00277x - 0.0339$<br>(0.990) |
| 50-percent hatch | 12.76 | $y = 0.00184x - 0.0235$<br>(0.972) | 12.18 | $y = 0.00184x - 0.0224$<br>(0.994) |
| Onset of retinal pigmentation | 12.89 | $y = 0.00162x - 0.0209$<br>(0.900) | 12.52 | $y = 0.00147x - 0.0184$<br>(0.974) |
| Light retinal pigmentation | 12.60 | $y = 0.00131x - 0.0164$<br>(0.983) | 11.14 | $y = 0.00113x - 0.0126$<br>(0.970) |
| Even retinal pigmentation | 12.15 | $y = 0.00110x - 0.0134$<br>(0.986) | 10.14 | $y = 0.000904x - 0.00917$<br>(0.957) |
| Initial jaw movement | 13.03 | $y = 0.000877x - 0.0115$<br>(0.987) | 11.01 | $y = 0.000670x - 0.00738$<br>(0.958) |
| *Mean* | *12.62* | | *11.52* | |
| *Standard deviation* | *0.27* | | *0.77* | |

ful hatching was observed. It appears, therefore, that the upper thermal limit for successful embryonic development of FLMB and F × N embryos is 0.5°–1.0°C higher than that for the NLMB and N × F embryos.

## Thermal Requirements of Embryogenesis

Using the overall $\alpha$-threshold temperatures calculated for the NLMB and N × F embryos and for the FLMB and F × N embryos, 12.62 ± 0.27 and 11.52 ± 0.77, respectively, the numbers of thermal developmental units (TDU) required to reach each of 22 development stages were calculated and are shown in Table 3. For the first 12 stages (mid-blastula through end of hatching), embryos from all stocks required comparable thermal input (TDU). However, for the remainder of development, the FLMB and F × N embryos required substantially greater thermal input (TDU) than did the NLMB and N × F embryos, ranging from 11.3 percent more for the onset of retinal pigmentation to 29.0 percent more for the final yolk absorption stage.

## DISCUSSION

The environmental thermal regimes which exist among the aquatic communities throughout the United States are extremely varied. Temperature plays a potentially major role in the processes of natural selection, genetically tailoring stocks of largemouth bass to specific environments (Childers 1975). Genetic differences between the two subspecies of largemouth bass, *M. s. salmoides* and *M. s. floridanus*, have been assessed and documented (Philipp et al. 1981, 1982, 1983). Indeed, a variety of physiological and behavioral differences most likely result from these genetic differences, each stock reacting somewhat differently to thermal conditions. Because these physiological and genetic differences among the two subspecies and their hybrids determine their relative fitness in a given environ-

Table 3. — Developmental unit requirements of the four stocks.

| Developmental Stages | Embryos of the NLMB and N × F $F_1$ Hybrid (SD) | Embryos of FLMB and F × N $F_1$ Hybrid (SD) |
|---|---|---|
| Mid-blastula | 69 (14) | 53 (11) |
| Half epiboly | 123 (29) | 122 (24) |
| Yolk plug | 166 (23) | 158 (23) |
| Initial body axis | 197 (23) | 193 (22) |
| 10 somites | 249 (36) | 240 (19) |
| 15 somites | 278 (33) | 275 (20) |
| 20 somites | 312 (37) | 310 (19) |
| 25 somites | 345 (30) | 340 (18) |
| Heartbeat | 379 (41) | 385 (18) |
| Begin hatch | 503 (48) | 508 (17) |
| 50-percent hatch | 556 (48) | 576 (17) |
| End hatch | 619 (53) | 660 (13) |
| Onset of retinal pigmentation | 670 (44) | 746 (53) |
| Light retinal pigmentation | 769 (44) | 851 (58) |
| Even retinal pigmentation | 865 (54) | 993 (75) |
| Initial jaw movement | 1,199 (77) | 1,452 (122) |
| Onset of body pigmentation | 1,318 (89) | 1,574 (136) |
| Red spleen formation | 1,372 (110) | 1,674 (135) |
| Begin swim-up | 1,501 (132) | 1,833 (111) |
| Begin free swimming | 1,715 (185) | 2,136 (159) |
| Active free swimming | 1,873 (208) | 2,417 (177) |
| Yolk absorbed | 2,031 (229) | 2,620 (203) |

ment, a quantitative assessment of thermal response differences among these stocks is critically needed for effectively formulating present and future management programs for largemouth bass.

Although Swingle (1956) reported that most largemouth bass spawning occurs between 68° and 75°F (20°–24°C), Chew (1974) documented spawning of FLMB in Lake Weir, Florida, at 59°F (15°C). Fluctuations in water temperature during the spring spawning season are usually not as severe in lakes in peninsular Florida as they are in lakes in more northerly regions. Largemouth bass spawns in Florida lakes during the earliest portion of the seasonal spawning period may be less likely to result in the exposure of eggs or embryos to very cold temperatures (<12°C) than would correspondingly early spawns in northern regions. It has been suggested that, in mixed populations, the Florida subspecies tends to spawn earlier in the season, at lower temperatures, than does the northern subspecies of largemouth bass (Hunsacker & Crawford 1964; Bottroff & Lembeck 1978; Moyle & Holzhauser 1978). Observations of spawning in ponds at the Illinois Natural History Survey during 1981 agreed with this suggestion (unpublished results); further experimentation is currently under way to verify this finding.

Interestingly, the $\alpha$-threshold temperature of development of the FLMB (11.52 ± 0.77) is significantly lower than that of the NLMB (12.62 ± 0.27). This relationship suggests a survival strategy of delayed spawning in the northern subspecies which presumably reflects a more variable, lower mean water temperature during spawning periods in the north. In addition, the northern subspecies apparently can use environmental incubation temperatures more efficiently. This use is evidenced by the significantly lower number of thermal developmental units required by NLMB embryos to reach the free swimming and actively feeding stage (2,031 ± 229) than that required by the FLMB (2,620 ± 203). Only at temperatures below about 16.2°C would FLMB eggs require less incubation time than NLMB eggs to reach the free swimming and actively feeding stage. At "normal" incubation temperatures NLMB embryos reach this stage sooner than do FLMB embryos. For example, at 20°C NLMB embryos would reach the free swimming and actively feeding stage at 272 hours, whereas the FLMB would require 309 hours to reach this stage. This more rapid development gives NLMB embryos a clear advantage over FLMB embryos at temperatures normally encountered during incubation periods in the wild (17°–25°C).

Interestingly, in comparing the embryological development of the two subspecies, major differences in numbers of thermal devlopmental units required occur at retinal pigmentation and later. These periods of embryonic development are associated with organogenesis and are periods during embryogenesis in which many of the genes encoding metabolic enzymes become activated (Philipp et al. 1979). This observation is consistent with the hypothesis that many of the metabolic processes up to the retinal pigmentation period may be under the control of maternal enzymes or m-RNA molecules synthesized during oogenesis. This observation also suggests that the two subspecies may have diverged in certain of their gene regulatory processes and now respond differently to temperature. The differences in the initial timing and levels of enzyme expression in developing embryos of these four stocks (NLMB, N × F, F × N, and FLMB) strongly support this suggestion (Philipp et al. 1983; Parker, Philipp, & Whitt unpublished results).

The two subspecies also differ in hatching success at various incubation temperatures. The peak of successful hatching for the NLMB occurs at lower temperatures (17°–22°C) than that for the FLMB (21°–24°C). In addition, the FLMB embryos apparently survive higher incubation temperatures than do the NLMB (Fig. 2). These relationships probably provide the NLMB and FLMB embryos an advantage in their respective environments.

It is interesting that the N × F embryos have consistently lower hatching percentages than their thermal counterpart NLMB embryos but that the opposite holds true for the F × N and FLMB embryos (Table 1). This set of relationships is an example of the inherent differences between reciprocal hybrids. We have postulated that these nonadditive asymmetrical responses by reciprocal hybrids result from differences in the interactions of the paternal genes with the maternal gene effector molecules (Whitt et al. 1977; Philipp et al. 1983).

Our analyses reveal that the developing embryos of NLMB and FLMB react differently to different temperatures. We feel that these differences have resulted from these two subspecific genomes having evolved independently in response to different thermal selective pressures. We postulate that to better survive colder climates, NLMB have evolved a reproductive strategy of delayed spawnng until they encounter higher temperatures. This strategy helps to prevent premature spawns, which could be destroyed by severe cold. In addition, NLMB have evolved schedules of embryonic gene expression, and thus mechanisms of controlling embryonic metabolism and morphogenesis, that operate efficiently and rapidly at lower temperatures. These patterns of gene expression also allow NLMB embryos to reach maximal hatching rates at lower temperatures than those required by FLMB embryos. However, during the protracted spawning seasons in peninsular Florida, early spawns produce individuals as much as 3 months earlier than late spawns. FLMB appear to have evolved a reproductive strategy which allows them to spawn at lower temperatures than those at which NLMB spawn. These early fish have distinct competitive advantages over fish spawned later. FLMB embryos have also evolved an increased tolerance to incubation temperatures higher than those of NLMB embryos. Thus, FLMB embryos are better able to tolerate the warm water temperatures found in peninsular Florida during the largemouth bass spawning season.

The divergence of developmental response to temperature in the two subspecies of largemouth bass has significant implications for management programs. Fitness probably varies greatly, depending upon the geographic location of the population, the physical characteristics of the body of water being considered, and the weather conditions during a given spawning season. However, it is not unreasonable to assume that, in the long run, stocks of largemouth bass introduced into inappropriate thermal environments will not perform as well as stocks which are introduced into thermal environments for which they have been genetically tailored. Our findings support the recommendation that management programs which result in mixing the two subspecies be discontinued. Precautions must be taken to protect the genetic integrity of the two subspecies. Specifically, we recommend that no largemouth bass containing any portion of the genome of the Florida subspecies be propagated for introduction into waters north of the intergrade zone as described by Philipp et al. (1981, 1982, 1983). We also recommend, of course, that the introduction of largemouth bass containing any portion of the genome of the northern subspecies into waters of pensinsular Florida be prohibited.

For maximum effectiveness, it is imperative that sound genetic principles be incorporated into current and future fisheries management programs (Smith & Chesser 1981; Philipp et al. 1981, 1982, 1983). Individual genetic stocks which constitute a species must be identified, characterized, and recognized as distinct units requiring individual consideration in management efforts. The genetic integrity of discrete stocks must be preserved, because as

Ryman (1981) has so aptly stated, "Genetic variation in natural populations constitutes a biological resource that must be properly managed so as not to reduce future opportunities for use of the resource."

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# Evolution of Reproductive Behaviors in Percid Fishes

Lawrence M. Page

Percid fishes are freshwater derivatives of a marine perciform, perhaps an anadromous serranid (McCully 1962; Collette & Bănărescu 1977). They appear to be relatively recent (i.e., most evolved during the Pliocene or later) but have undergone a tremendous radiation in North America, where they now comprise about 151 species in five genera. Among North American freshwater fishes, only minnows (Cyprinidae), with about 225 species, are more diverse. Together, percids and minnows constitute almost half of the temperate North American freshwater fish fauna. In addition to being diverse groups, these fishes often occur in large populations and are important in determining the ecological characteristics of North American streams and lakes. Elsewhere, percids are present only in temperate Eurasia, where there are 14 species in six genera. Two genera, *Stizostedion* and *Perca*, occur in both North America and Eurasia (Table 1).

Several reasons exist for studying the reproductive habits of organisms. Among these are that (1) reproductive habits are inherently interesting; (2) reproduction is that activity toward which all life processes ultimately are directed and, therefore, understanding its variations is important if we wish to protect or manage species; and (3) reproductive characteristics provide information useful in estimating evolutionary (phylogenetic) history. Percids are especially interesting in this last regard because, as a recent and diverse group, transitions among their various types of reproductive behaviors remain evident today. Reconstructing the evolutionary history of reproductive behaviors of percids results in a better understanding of the relationships among species.

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## TYPES OF REPRODUCTIVE BEHAVIORS

Accompanying the evolution of a large diversity of percids has been the evolution of a variety of reproductive

Table 1. — Percid taxa and their distributions.

| Taxa | Number of Species | Distribution |
|---|---|---|
| Etheostomatinae | | |
| Luciopercini | | |
| *Stizostedion* | 5 | Holarctic |
| Etheostomatini | | |
| *Percina* | ca. 38 | Nearctic |
| *Ammocrypta* | 7 | Nearctic |
| *Etheostoma* | ca. 103 | Nearctic |
| Romanichthyini | | |
| *Zingel* | 3 | Palearctic |
| *Romanichthys* | 1 | Palearctic |
| Percinae | | |
| *Percarina* | 1 | Palearctic |
| *Perca* | 3 | Holarctic |
| *Gymnocephalus* | 4 | Palearctic |

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strategies, and in the most advanced states, parental care of the eggs. Among the 76 species of percids for which spawning behaviors are known, six types of behavior are recognized, some of which can be subdivided further, as discussed below. These six types, named for the mode of egg-deposition, are termed (1) broadcasting, (2) stranding, (3) burying, (4) attaching, (5) clumping, and (6) clustering.

## Broadcasting

Broadcasting is the primitive mode of reproductive behavior among fishes and is retained in primitive percids. Eggs and sperm are discharged in large numbers, often in a frenzy of activity involving several individuals. A coarse substrate, usually composed of rocks or plants, is chosen to provide crevices and other hiding places for the fertilized eggs. In its most primitive state, broadcasting makes no other behavioral provisions for the eggs, either before or after spawning.

*Stizostedion vitreum* (Mitchill) and *S. canadense* (Smith) broadcast their eggs between March and June in streams and in areas of lakes with sufficient water movement to ventilate the eggs (Eschmeyer 1950; Nelson 1968). Spawning usually occurs in the evening (Ellis & Giles 1965) or at night (Eschmeyer 1950), and territories are not established (Ellis & Giles 1965). Courtship consists of an individual of either sex approaching another individual from behind or from the side and pushing against it. The approached fish either withdraws or, if sexually responsive, makes quick darts forward and upward. This increased activity often elicits the attention of other individuals, and soon a compact group forms, which periodically rushes forward and upward. Eggs and sperm are released during a forward rush of activity (Ellis & Giles 1965). Spawning groups vary from two individuals to several individuals of both sexes (Fig. 1). Eggs are adhesive for a few hours, and they may adhere to rocks or plants for a short time; ultimately they fall to the bottom and into interspaces among the components of the substrate (Fig. 2), where they presumably are less exposed to predation (Colby et al. 1979). *S. marinum* (Cuvier) and *Percarina demidoffi* Nordmann appear to exhibit similar, perhaps identical, behavior (Berg 1949) although descriptions of spawning are vague.

*Stizostedion lucioperca* (Linnaeus) exhibits a modification of this behavior in that eggs and sperm are broadcast over a circular pit previously constructed by the male. The pit is lined with gravel, shells, or plant material (often roots) and is guarded before and after spawning by the male, who also fans the fertilized eggs (Kryzhanovshy et al. 1953). Mating in this more special-

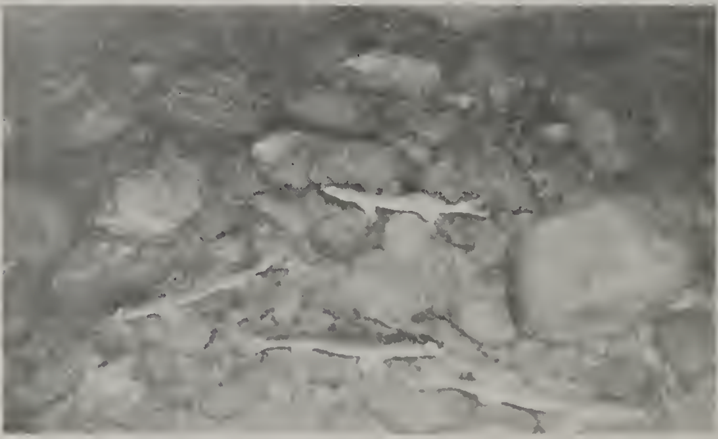

Fig. 1. – *Stizostedion vitreum* congregated on spawning grounds at Lake Gogebic, Michigan, 4 May 1948. From Eschmeyer (1950). (Photo provided by the Institute for Fisheries Research, Fisheries Division, Michigan Department of Natural Resources.)

Fig. 2. – Eggs of *Stizostedion vitreum* on spawning ground at Lake Gogebic, Michigan, 12 May 1948. From Eschmeyer (1950). (Photo provided by the Institute for Fisheries Research, Fisheries Division, Michigan Department of Natural Resources.)

ized, nesting broadcaster may be monogamous (Deedler & Willemsen 1964).

Broadcasters

Group A. Spawn over open substrate
  *Stizostedion vitreum* (Eschmeyer 1950)
  *S. canadense* (Nelson 1968)
  *S. marinum* (Berg 1949)
  *Percarina demidoffi* (Berg 1949)
Group B. Spawn over male-constructed pit
  *S. lucioperca* (Kryzhanovshy et al. 1953)

## Stranding

Stranders have the unique habit of encasing their eggs in long gelatinous strands. A ripe female is followed by several males through beds of vegetation (sometimes tree roots or debris) in slowly flowing or standing water. The males release sperm as she extrudes a convoluted egg strand (Worth 1892; Treasurer 1981). The strand is gelatinous, transparent, hollow, and arranged in bellowslike transverse folds. When first laid, the shape of the egg mass is similar to that of the ovarian cavity (Fig. 3), but eventually it stretches (Fig. 4) and may reach a length of 2.4 m and a width of 10 cm (Hardy 1978). Egg stranding is known to occur in *Perca flavescens* (Mitchill) (Worth 1892; Harrington 1947; Hergenrader 1969) and *P. fluviatilus* Linnaeus (Seeley 1886:27; Wheeler 1969:322; Treasurer 1981). It also may occur in *Gymnocephalus cernua* (Linnaeus), as described by Seeley (1886:36) and Wheeler (1969:321), although some authors (e.g., Nikol'skii 1961:369; Muss 1978:161) discuss spawning in *Gymnocephalus* without mentioning egg strands.

Stranders

*Gymnocephalus cernua* (Seeley 1886)
*Perca flavescens* (Worth 1892)
*P. fluviatilus* (Seeley 1886)

Stranding is probably a direct derivative of broadcasting. The eggs become encased in gelatin in the ovaries and when emitted remain part of a cohesive mass rather than becoming independently scattered. The derivation of stranding from percid spawning behaviors other than broadcasting is less likely, because each is specialized in a way that seems to preclude the evolution of stranding.

For a female to put all of her eggs in one highly visible basket, which stranding certainly does, and then abandon them would seem to be a strategy quickly selected against unless the eggs somehow are protected intrin-

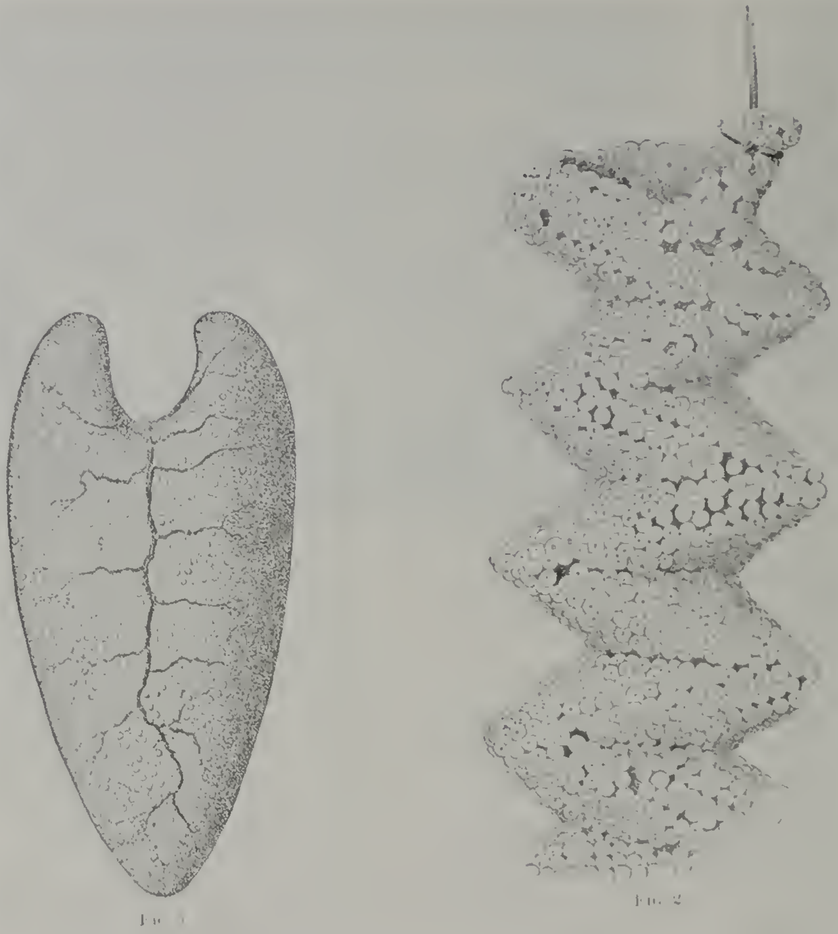

Fig. 3. – Eggs of *Perca flavescens* encased in ovaries (left) and in gelatinous strands after being spawned (right). From Worth (1892).

sically against predation and disease. Having toxic, or at least distasteful, eggs would be an obvious strategy, but observations by Seeley (1886:27) of predation by "birds and various fishes" on perch eggs put this method in doubt. Treasurer (1983) reported low mortality of perch eggs and attributed it to the improved ventilation and midwater position (thereby avoiding siltation) of the strand.

### Burying

Egg-burying behavior is similar to broadcasting except for the important distinction that the release of eggs occurs just below, rather than above, the surface of the substrate. In egg burying the female works her body partially below the surface of the substrate and, with her genital papilla buried and a male mounted on her back, expels eggs (Fig. 5). The substrates usually used are loose gravel, sand, or mixed gravel and sand. Egg burying is characteristic of many darters, including all species of *Percina* for which spawning observations have been published and many species of *Etheostoma*. Some egg buriers are thought to be territorial (Winn 1958), but other than the indirect protection associated with territoriality, eggs receive no parental care. Among darters, burying represents the primi-

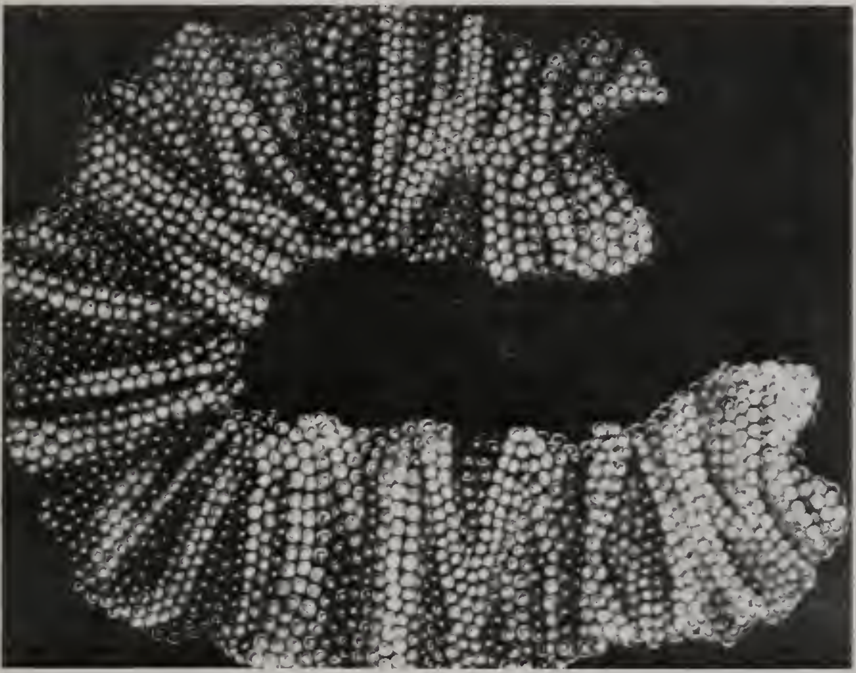

Fig. 4. – Egg strand of *Perca flavescens*. From Pearse & Achtenberg (1921).

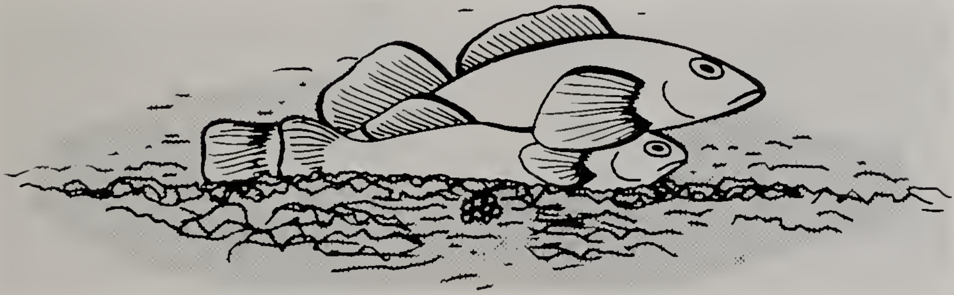

Fig. 5. – Egg-burying behavior. With a male mounted on her back, a partially buried female deposits eggs below the surface of the substrate. Eggs are fertilized as they are laid and then are abandoned by both parents.

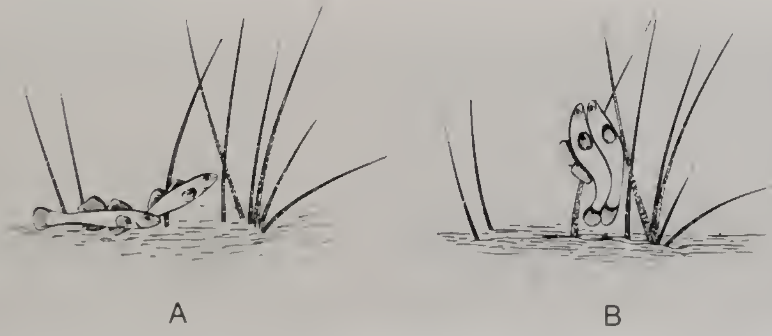

Fig. 6. – Egg-attaching behavior. (A) The female selects the site of egg deposition. (B) The male mounts the female and releases sperm as eggs are attached to plants. The eggs subsequently are abandoned.

tive form of reproductive behavior; among percids, it represents an egg-hiding modification of broadcasting behavior.

Buriers

*Percina (Alvordius) maculata* (Petravicz 1938)
*P. (A.) peltata* (New 1966)
*P. (A.) notogramma* (Loos & Woolcott 1969)
*P. (Ericosma) evides* (Page et al. 1982)
*P. (Hypohomus) aurantiaca* (Howell 1971)
*P. (Cottogaster) copelandi* (Winn 1953)
*P. (Percina) caprodes* (Winn 1958)
*Etheostoma (Litocara) nianguae* (Pflieger 1978)
*E. (Psychromaster) tuscumbia* (Koch 1978)
*E. (Etheostoma) tetrazonum* (Pflieger 1978)
*E. (E.) variatum* (May 1969)
*E. (Doration) stigmaeum* (Winn 1958)
*E. (Nothonotus) juliae* (James 1983)
*E. (N.) rufilineatum* (Stiles 1972)
*E. (N.) camurum* (Mount 1959)
*E. (N.) bellum* (W. D. Voiers personal communication)
*E. (N.) tippecanoe* (Trautman 1981)
*E. (Fuscatelum) parvipinne* (B. M. Burr personal communication)
*E. (Ozarka) cragini* (Distler 1972)
*E. (Oligocephalus) spectabile* (Winn 1958)
*E. (O.) caeruleum* (Winn 1958)
*E. (O.) radiosum* (Scalet 1973)
*E. (O.) swaini* (Ruple et al. 1984)

## Attaching

Attaching behavior is a derived behavior known among percids only in the genus *Etheostoma*. The female selects the site of egg deposition (presumably in some species within a male's territory), typically a plant or large rock, and with the male following her, elevates to the site. As she does so, the male follows and mounts, the two vibrate, and eggs and sperm are released (Fig. 6). Usually one to three adhesive eggs are released during each spawning act and are pushed by the female onto a plant, rock, or other object. Attaching eggs to plants seems to involve behavior identical to that of attaching eggs to rocks; the substrate used is that which is readily available in the habitat. Eggs are abandoned and receive no direct parental care, although as in some burying species, territorial behavior may provide some protection.

Attachers

*Etheostoma (Etheostoma) blennioides* (Fahy 1954)
*E. (Nanostoma) zonale* (Winn 1958)
*E. (N.) coosae* (O'Neil 1981)
*E. (N.) baileyi* (Page personal observation)
*E. (N.) simoterum* (Page & Mayden 1981)
*E. (N.) duryi* (Page et al. 1982)
*E. (N.) barrenense* (Winn 1958)
*E. (N.) rafinesquei* (Winn 1958)
*E. (N.)* sp. (Red Snubnose) (B. M. Burr personal communication)
*E. (N.)* sp. (Lowland Snubnose) (B. M. Burr personal communication)
*E. (Ioa) vitreum* (Winn & Picciolo 1960)
*E. (Vaillantia) chlorosomum* (Page et al. 1982)
*E. (Belophlox) okaloosae* (Collette & Yerger 1962)
*E. (Villora) edwini* (Williams 1976)
*E. (Ozarka) boschungi* (Boschung 1979)
*E. (O.) trisella* (W. C. Starnes personal communication)
*E. (Oligocephalus) lepidum* (Strawn 1956)
*E. (O.) asprigene* (Page et al. 1982)
*E. (O.) grahami* (Strawn 1956)
*E. (O.) ditrema* (Seesock et al. 1978)
*E. (Boleichthys) exile* (Winn 1958)
*E. (B.) fusiforme* (Fletcher 1957)
*E. (B.) gracile* (Braasch & Smith 1967)
*E. (B.) proeliare* (Burr & Page 1978)
*E. (B.) fonticola* (Schenck & Whiteside 1977)
*E. (B.) microperca* (Burr & Page 1979)

The presence of both egg-burying and egg-attaching species within three subgenera of *Etheostoma (Etheostoma, Ozarka,* and *Oligocephalus)* suggests that egg attaching is derived directly from egg burying and has arisen independently in several unrelated groups of darters. In fact, at least two species which usually attach their eggs have been observed to bury eggs under certain conditions (Petravicz 1936; Page & Mayden 1981). Egg attaching apparently also has arisen independently among species within subgenera; its distribution among species of *Ozarka* is inconsistent with the distribution of morphological synapomorphies (Fig. 7).

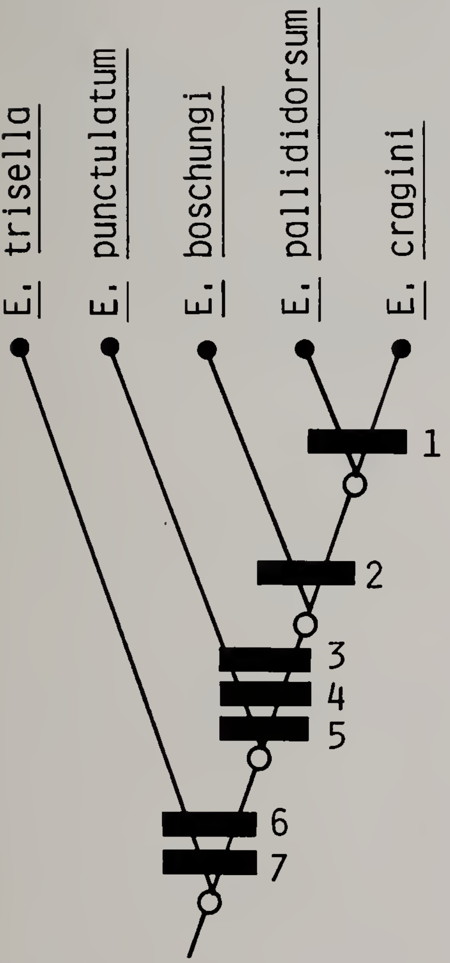

Fig. 7. – Hypothesized phylogenetic relationships among species of *Ozarka*. Synapomorphies (black rectangles) are (1) 25 or fewer pored lateral-line scales, (2) seven infraorbital pores, (3) interrupted supratemporal canal, (4) incomplete lateral line, (5) bright orange margin on the first dorsal fin, (6) bright orange venter on the breeding male, (7) heavily mottled body. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma (Oligocephalus) whipplei* and *E. (Belophlox) fricksium*.

*E. cragini* Gilbert buries its eggs, but *E. boschungi* Wall and Williams and *E. trisella* Bailey and Richards attach their eggs to plants (Boschung 1979; W. C. Starnes personal communication). If the phylogeny based on morphology (Fig. 7) is accurate, *E. boschungi* and *E. trisella* must have evolved egg-attaching behavior independently of one another. The fact that *E. trisella* attaches its eggs to vegetation in headwaters (even seepages) (W. C. Starnes, personal communication) was a major factor in placing it in the subgenus *Ozarka* with *E. boschungi*, which has essentially the same spawning requirements and behavior (Boschung 1979; Williams & Robison 1980). Independent derivation of this behavior in the two species weakens the argument for their close relationship to one another.

The breeding behaviors of too few species of the subgenus *Etheostoma* are known to compare their distributions with a phylogeny based on morphology. However, it is interesting that the two known buriers [*E. variatum* Kirtland and *E. tetrazonum* (Hubbs and Black)] are in the *E. variatum* species group [including also *E. euzonum* (Hubbs and Black), *E. osburni* (Hubbs and Trautman), and *E. kanawhae* (Raney)], and the only known attacher, *E. blennioides* Rafinesque, is a member of the second major lineage [including *E. rupestre* Gilbert and Swain, *E. inscriptum* (Jordan and Brayton), *E. thalassinum* (Jordan and Brayton), *E. swannanoa* Jordan and Evermann, *E. blennius* Gilbert and Swain, and *E. histrio* Jordan and Gilbert], all of which eventually may be shown to be egg attachers. *E. sellare* (Radcliffe and Welsh), the sole member of the third major lineage in the subgenus, is a highly distinctive (Knapp 1976; Page 1981) species on the verge of extinction. It has a flattened genital papilla (Knapp 1976) similar to those of egg-clumping and egg-clustering species (Page & Swofford 1984). If *E. sellare* is found to belong to one of these latter behavioral groups, it could be of major significance in efforts to protect the species from extinction. Suitable spawning sites may be a limiting factor for the only extant population of *E. sellare*.

## Clumping

Egg clumping was first reported in 1939 for *E. maculatum* Kirtland (Raney & Lachner 1939) but was unreported for other darters until observed in 1981 in *E. aquali* Williams and Etnier and *E. microlepidum* Raney and Zorach (Page et al. 1982). In preparation for spawning, the male selects a cavity under a large rock as a territory and future nesting site. Ultimately, a female swims into the cavity being guarded by the male, wedges herself into the interface between the stone and the gravel substrate beneath the stone, and deposits eggs. As she does so, they are fertilized by the male. After spawning, the female leaves, and the male remains to guard the clump of eggs (Fig. 8). The adhesive eggs adhere to both the nest stone and the underlying substrate material; if a stone is lifted from the water, a clump of adhesive eggs remains attached to it (Fig. 9).

Egg clumping is known only among species of the subgenus *Nothonotus* of *Etheostoma*.

Clumpers

*Etheostoma (Nothonotus) maculatum* (Raney & Lachner 1939)
*E. (N.) aquali* (Page et al. 1982)
*E. (N.) microlepidum* (Page et al. 1982)

Egg clumping is almost certainly a direct derivative of the egg-burying behavior (Page et al. 1982) characteristic of other species of *Nothonotus* [known in *E. juliae* Meek, *E. rufilineatum* (Cope), *E. camurum* (Cope), and *E. tippecanoe* Jordan and Evermann]. The transition from burying in some species of *Nothonotus* to clumping in others requires only that the male establish a territory beneath a stone and that a female deposit her eggs in the interface area between the stone and the underlying substrate.

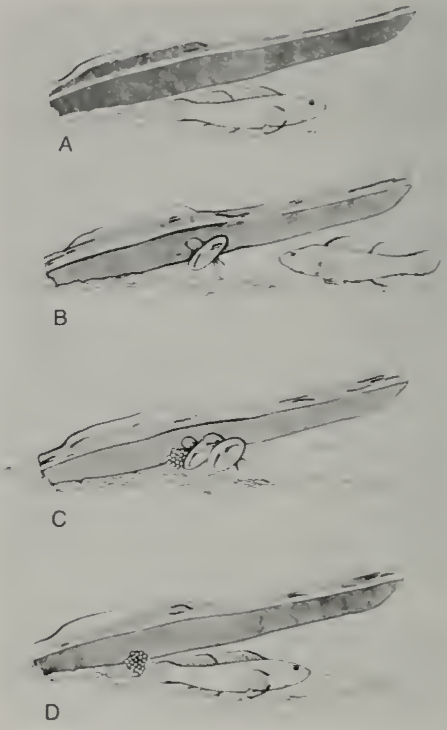

Fig. 8. – Egg-clumping behavior. (A) The male establishes a territory centered under a large stone. (B) The female enters the territory and wedges herself between the stone and the underlying substrate. (C) The male positions himself next to the female and fertilizes eggs as they are released by the female. (D) The male remains to guard the clump of eggs.

With 14 described and 1 undescribed species, the subgenus *Nothonotus* is one of the two largest subgenera of darters, and intrasubgeneric relationships are unclear. The egg-clumping species are members of the *E. maculatum* lineage within the subgenus (Fig. 10), but it is unknown at present at what point on the lineage egg clumping arose. *E. rufilineatum* has been observed to bury its eggs (Stiles 1972), and although spawning was not observed, Bryant (1979) felt confident that *E. acuticeps* Bailey also buries its eggs. Spawning behavior data on *E. rubrum* Raney and Suttkus and *E. moorei* Raney and Suttkus should pinpoint the origin of egg clumping in *Nothonotus*.

Although *Etheostoma sanguifluum* (Cope) has been considered a subspecies of *E. maculatum* Kirtland by some

Fig. 9. – A male *Etheostoma microlepidum* and his clump of eggs on the underside of a stone removed from East Fork Stones River, Rutherford County, Tennessee, on 6 May 1981. The male was guarding the eggs prior to their removal from the stream.

authors (Zorach & Raney 1967; Williams & Etnier 1978), the distinctive pigmentation of the first dorsal fin (especially the bright red spots at the front and rear of the fin) of the male of *E. sanguifluum* is shared with *E. aquali* Williams and Etnier but is absent in all other species of the subgenus *Nothonotus*. Recognition of a closer relationship between *E. sanguifluum* and *E. aquali*, than of either taxon to *E. maculatum* (Fig. 10), requires the elevation of *E. sanguifluum* to specific status. The form heretofore known as *E. maculatum vulneratum* (Cope) also possesses the distinctive dorsal fin pigmentation and should be named *E. sanguifluum vulneratum* (Cope).

## Clustering

The first report of egg-clustering behavior in darters was by Seal in 1892 in a report on *E. olmstedi* Storer. Since then it has been documented in an additional 15 species in the subgenera *Boleosoma* and *Catonotus* of *Etheostoma* listed below.

The male of an egg-clustering species establishes a territory centered about the cavity under a large (usually flat) stone. The cavity and the underside of the stone are cleared of silt and debris by fin-wagging activities of the male. A ripe female enters the cavity and, following courting by the male, rolls to one side and, once inverted, rises and lays eggs on the underside of the stone. The male inverts and fertilizes the eggs, which are arranged by the female in a single-layer cluster (i.e., eggs are rarely laid on top of one another) on the stone. The female leaves; other females sequentially may add eggs to the nest. The male remains and guards the eggs to hatching (Fig. 11). In species of *Boleosoma*, a log may be substituted for a stone.

Egg clustering is similar to egg clumping in that eggs are amassed under a stone and guarded by the male.

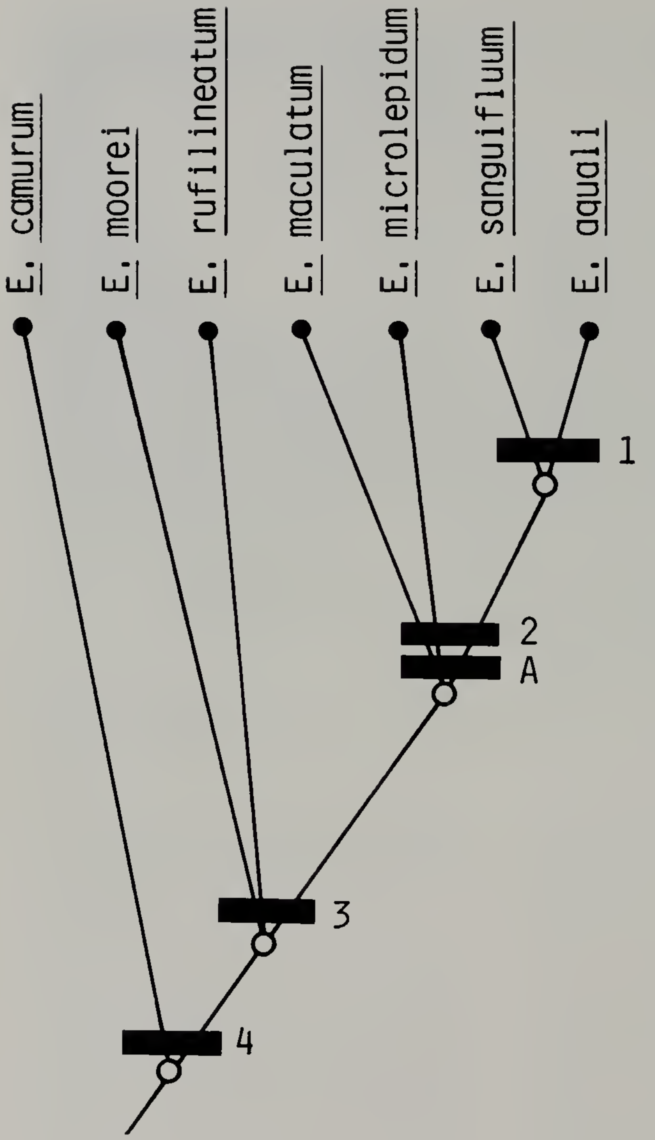

Fig. 10. – Hypothesized phylogenetic relationships among some of the species of *Nothonotus*. Synapomorphies (black rectangles) are (1) dorsal fin with two red spots at the front, one red spot at the rear, (2) haloed red spots on the side of the male, (A) egg-clumping behavior, (3) black spots on fins of the female, and (4) red spots on the side of the body. Synapomorphous Character states were identified by outgroup comparisons to *Etheostoma (Nothonotus) tippecanoe*, *E. (N.) juliae* and *E. (N.) acuticeps*.

It is dissimilar, and appears to be "perfected," in that every egg is exposed and can be tended to individually by the guarding male (Fig. 12).

The derivation of egg clustering from darters which attach their eggs to stones requires only that (1) eggs are laid on the underside rather than the tops and sides of rocks, (2) eggs are clustered in close proximity to one another rather than distributed over a broad area, and (3) the male remains and guards the eggs. Laying eggs on the underside rather than on more exposed areas of rocks probably exposes them to fewer predators although some potential predators, e.g., crayfishes and caddisflies (Brigham et al. 1982:9.6), are common under rocks. Once the eggs under the stone are guarded by the male, the survival rate undoubtedly increases dramatically, and such a concentration of eggs is quickly selected for.

Variation in behavior divides egg-clustering species into three groups: (A) those in which both male and female invert only long enough to lay

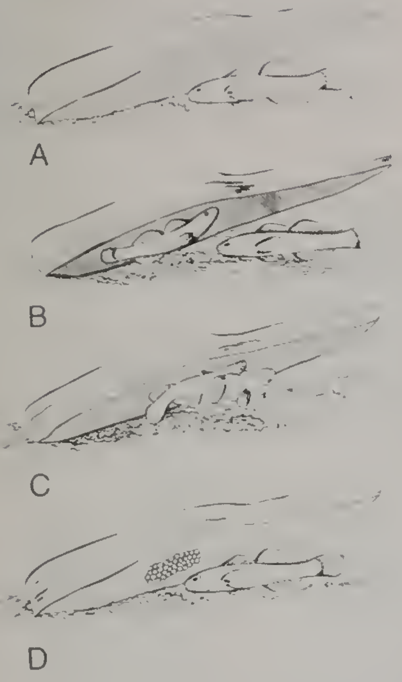

Fig. 11. – Egg-clustering behavior. (A) The male establishes a territory centered under a large stone. (B) The female enters the territory and selects a site for egg deposition on the underside of the stone. (C) The female inverts, rises, and deposits eggs on the stone; as she does so, the male follows and fertilizes the eggs. (D) The male remains to guard the cluster of eggs.

and fertilize each release of eggs (usually 1-5 eggs); (B) those in which the female, once inverted, remains inverted for a prolonged period of egg laying (several minutes to a few hours) but the male only briefly (a few seconds) and periodically inverts; and (C) those in which both male and female remain inverted for an extended period. Obviously, group B represents an advancement over group A, and group C represents an advancement over group B. Group A includes the primitive species of the subgenus *Catonotus*; B, the advanced species of *Catonotus* (Page 1975b); and group C, species of the subgenus *Boleosoma*. Winn (1958) distinguished between behavior types B and C.

Clusterers

Group A. Female and male briefly invert
- *E. (Catonotus) squamiceps* (Page 1974)
- *E. (C.) olivaceum* (Page 1980)
- *E. (C.) neopterum* (Page & Mayden 1979)[a]

Group B. Female only has prolonged inversion
- *E. (C.) flabellare* (Winn 1958)
- *E. (C.)* sp. = Duskytail darter (Etnier personal communication)[a]
- *E. (C.) kennicotti* (Page 1975a)
- *E. (C.) obeyense* (Page et al. 1981)[a]
- *E. (C.) virgatum* (Kornman 1980)[a]
- *E. (C.) smithi* (Page & Burr 1976)
- *E. (C.) striatulum* (Page 1980)[a]
- *E. (C.) barbouri* (Page et al. 1982)[a]

Group C. Female and male have prolonged inversions
- *E. (Boleosoma) olmstedi* (Atz 1940)
- *E. (B.) nigrum* (Winn 1958)[a]
- *E. (B.) podostemone* (Jenkins 1980)[a]
- *E. (B.) perlongum* (Lindquist et al. 1981)
- *E. (B.) longimanum* (Page et al 1981)[a]

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[a] Although known to be a clusterer, group assignment is predicted from the behavior of closest relatives and is not based on actual observations.

The phylogenetic sequence of breeding behaviors among *Catonotus* is concordant with a phylogeny of the subgenus based on morphology in that three synapomorphies unite the *E. flabellare* Rafinesque lineage as advanced and apart from the *E. squamiceps* Jordan species group (Fig. 13).

Both *Catonotus* and *Boleosoma* must have evolved from egg-attaching precursors. Although egg clustering itself could be considered a synapomorphy uniting these two subgenera, they differ markedly in their morphology and do not appear to be sister groups (Page 1981). *Boleosoma* shares derived characteristics with other groups of *Etheostoma* (Fig. 14) and almost certainly had an origin independent from that of *Catonotus*. It appears to be most closely related to *E. (Ioa) vitreum* (Cope), an egg-attaching species. The sister-group of *Catonotus* should first be sought among egg-attaching species; however, if the attaching precursor now is extinct, an egg-burying group may be the closest extant relative.

## EVOLUTION OF PERCID SPAWNING BEHAVIORS

Combining the evolutionary sequences discussed above produces the phyl-

Fig. 12. – Male *Etheostoma neopterum* and his cluster of eggs on the underside of a stone removed from Birdsong Creek, Benton County, Tennessee, on 15 April 1978. The male was guarding the eggs prior to their removal from the stream.

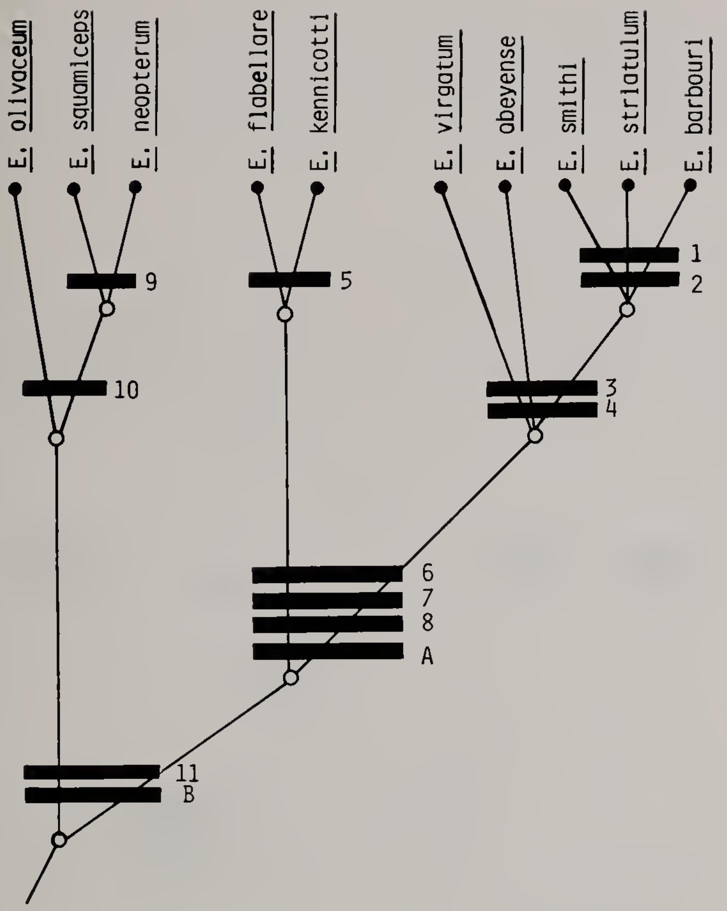

Fig. 13. – Hypothesized phylogenetic relationships among species of *Catonotus*. Synapomorphies (black rectangles) are (1) four infraorbital pores, (2) maximum standard length less than 50 mm, (3) bar pattern on the cheek, (4) blue-edged red fins on the breeding male, (5) large gold knobs on the first dorsal fin, (6) nape unscaled, (7) prepectoral area unscaled, (8) infraorbital canal widely interrupted, (A) type B clustering behavior (the female remains inverted during spawning), (9) infraorbital canal narrowly interrupted, (10) caudal peduncle with three black spots, (11) broad, flat nonbifurcate genital papilla on the female, (B) egg-clustering behavior. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma (Psychromaster) tuscumbia* and *E. (Fuscatelum) parvipinne*.

ogeny depicted in Fig. 15. There appear to be no reasonable alternatives to any of the transitions depicted. However, each type of behavior could have arisen, and in some instances almost certainly did arise, more than once. For example, although gamma clustering results from a modification of beta clustering, it does not mean that the only extant gamma-clustering group of darters (*Boleosoma*) arose from the only extant beta-clustering group (i.e., the *flabellare* group of *Catonotus*); rather, all alpha and beta precursors of *Boleosoma* are extinct.

The phylogeny (Fig. 15) supports the contention that darters, the most primitive of which are buriers, are derivatives, and probably the sister group, of *Stizostedion*. This position disagrees with the conclusions of Collette (1963) based on osteology, but it agrees with those of Hubbs (1971) based on the survival of intergroup percid hybrids. A phylogenetic classification necessitates the recognition of the subfamilies Etheostomatinae (containing the tribes Luciopercini, Etheostomatini, and Romanichthyini) and Percinae (Table 1).

Each step in the evolution of spawning behaviors represents, for the species in which it evolved, a survival advantage over its precursor. Pit broadcasting concentrates the eggs in an area subsequently guarded by the male

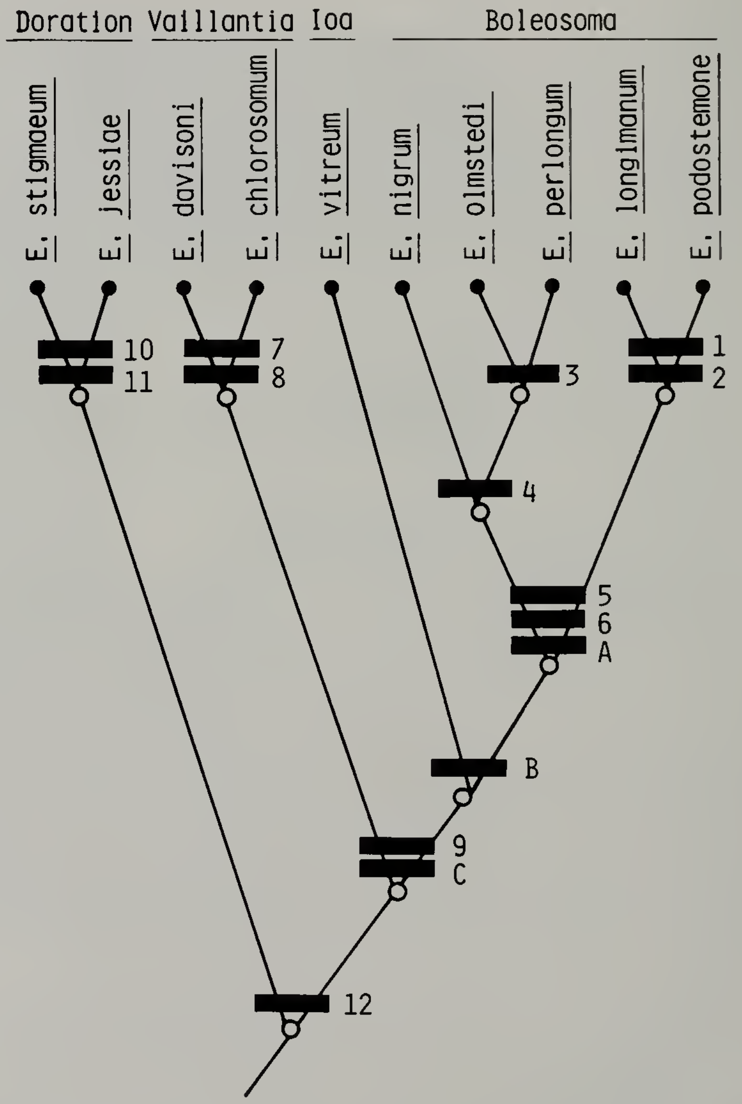

Fig. 14. – Hypothesized phylogenetic relationships among species of the subgenera *Boleosoma*, *Ioa*, *Vaillantia*, and *Doration*. Synapomorphies (black rectangles) are (1) broad branchiostegal membrane connection, (2) red-orange spots on the breeding male, (3) elongated second dorsal fin on the breeding male, (4) overall dusky breeding male, (5) bifurcate genital papilla on the female, (6) white knobs on paired fins, (A) egg-clustering behavior, (B) eggs attached to rocks, (7) black bridle around the snout, (8) extremely short second dorsal fin, (9) spatulate genital papilla on the female, (C) egg-attaching behavior, (10) blue bars on the adult male, (11) blue and red bands in the first dorsal fin of the adult male, (12) brown-black x/w marks on the body. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma (Psychromaster) tuscumbia* and *E. (Litocara) nianguae*.

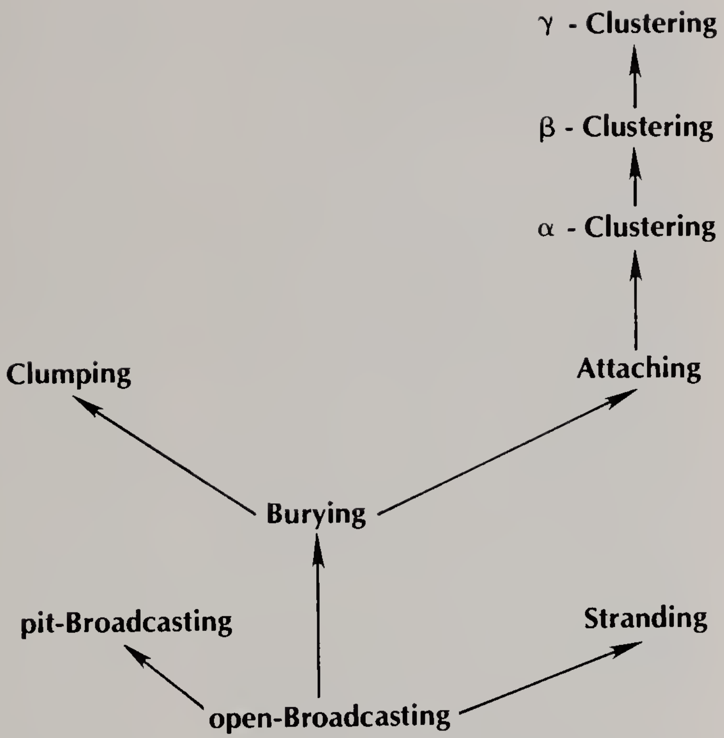

Fig. 15. – Hypothesized evolutionary relationships among percid breeding behaviors.

and thus increases the probability of their survival by reducing predation. Also, *S. lucioperca* males fan the eggs, presumably to prevent them from being covered by silt, and thereby reduce mortality due to anoxia.

Burying eggs reduces exposure to predators and probably to parasites, enhancing survivability. However, eggs can be buried only in flowing water habitats, usually in gravel but sometimes in sand, where burying does not subject the eggs to especially low oxygen levels such as would occur if eggs were buried in slow-flowing or standing water. Buriers are constrained behaviorally to flowing water and coarse substrates. Consequently, stream modifications, such as impoundments and channelization, prevent successful spawning by these species.

In the primitive state, species of *Nothonotus* bury their eggs in the sand-gravel mixture on the downstream side of a large stone in fast water. Clumping, as discussed above, evolved in a species of *Nothonotus* which buried its eggs under a partially elevated stone, thereby enhancing crypticity. The advantage of male egg guarding followed.

The derivation of attaching from burying (or from any other behavior) is difficult to envision. However, the presence of both behaviors within several (at least three) subgenera of *Etheostoma* leaves no doubt that one is derived directly from the other. The strong positive correlation between primitive morphology and burying (e.g., all species of *Percina* are buriers) and between advanced morphology and attaching (e.g., in the subgenus *Boleichthys*) clearly indicates that the direction is from burying to attaching. For darters living in slow-flowing or standing water (e.g., *Boleichthys* species), the advantage of attaching is obvious; with demersal and adhesive eggs, the only alternatives to attaching are burying eggs in an oxygen-poor substrate (often rotting vegetation and mud) or migrating to suitable habitats for burying. Similarly, species living in bedrock pools [e.g., *E. simoterum* (Cope)] where little suitable egg-burying substrate exists, were probably better fit after they changed to egg attaching (Page & Mayden 1981). That so many species have converted from burying to attaching (at least 9 of the 13 subgenera of *Etheostoma* for which the spawning behavior of at least one species is known, are known to contain egg-attaching species) seems to reflect the fact that few alternatives exist. Clumping is an alternative, but it was available evolutionarily only to species which bury their eggs near (and eventually under) large stones. Among darters, clumping evolved only in *Nothonotus*; other fishes with behavior similar to egg clumping in darters are species of *Cottus* (Smith 1923) and *Noturus* (Mayden & Burr 1981). The evolution of egg attachment permitted groups of darters to invade new habitats (e.g., bedrock pools, sand and mud bottomed pools, swamps) that otherwise could have been invaded only with periodic (presumably annual) emigrations into other habitats suitable for egg burying. This emigration would be difficult for advanced darters, which lack gas bladders. A few darters have followed the latter strategy [e.g., *Percina cymatotaenia* (Gilbert and Meek), a primitive darter which has a gas bladder and lives in vegetated backwaters, moves into riffles to spawn (Pflieger 1975: 299)]; however, the groups which live and spawn in the same habitat have been most successful in diversifying (e.g., *Boleichthys, Nanostoma*).

Clustering darters are sophisticated attachers which concentrate their eggs in a hidden space and then guard them through hatching. The single-layer arrangement of eggs permits the guarding male to tend each egg. Although the close proximity of the eggs promotes the spread of infection, and of predation if a predator succeeds in gaining access to the nest, the advantages of clustering apparently outweigh the disadvantages. Furthermore, males of both egg-clustering darters and egg-clustering minnows (*Pimephales*) develop swollen flesh on the head and nape during the breeding season. The swollen flesh is thought to have a secretory, presumably fungicidal or bactericidal, function related to protecting the eggs during nest guarding (Cross 1967; Smith & Murphy 1974). Clustering darters and minnows are some of the most widespread and abundant fishes [e.g., *Etheostoma nigrum* Rafinesque, *E. olmstedi, E. flabellare, Pimephales notatus* (Rafinesque), and *P. promelas* Rafinesque] in North America.

Two earlier discussions on the diversity and evolution of percid reproductive behaviors were those of Winn (1958) and Balon et al. (1977). The latter assigned percids to seven reproductive "guilds" that conceptually encompassed both spawning and ontogenetic characteristics. Species that herein are classified as open substrate broadcasters, stranders, and attachers are variously classified by Balon et al. (1977) as open substrate lithophils (rock spawners), phytophils (plant spawners), and phyto-lithophils. Buriers are termed brood hiding lithophils, and clumpers and clusterers are nest spawning speleophils (cave spawners). McElman (1983) argued subsequently that *S. vitreum* and *S. canadense* should be classified as litho-pelagophils because of the buoyancy, positive phototaxis, swimming ability, and surface suspension properties of their newly hatched young, and that *S. lucioperca* should be termed a phyto-pelagophil because of the swimming ability of its newly hatched young. Page & Swofford (1984) argued that Balon et al. (1977) assigned some darters [i.e., *P. caprodes* (Rafinesque), *E. blennioides, E. vitreum*, and possibly *P. shumardi* (Girard) and *Ammocrypta* spp.] to guilds incorrectly.

Winn (1958) dealt exclusively with darters and concentrated primarily on the 14 species for which he presented original data. He recognized the least complex behaviors as primitive and the most complex (especially clustering) as derived, and discussed these evolutionary trends: development of territoriality; use of substrates other than gravel for spawning; occupation of smaller streams; maturation of fewer, larger eggs; decrease in promiscuity; development of parental care; an increase in sexual dimorphism (including a relative increase in the size of the male); a decrease in body size; and a decrease in the age of sexual maturity from 2–3 years to 1 year. With data now available on many more species, these trends still seem accurately to characterize darter evolution, except that the only darters thought to be nonterritorial (and the only species in which females are larger than males) are species of advanced (i.e., *Ozarka* and *Boleichthys*), not primitive, subgenera, and sexual dimorphism in color is most extreme among egg buriers (Page 1983; Page and Swofford 1984), behaviorally the most primitive darters.

## LIFE HISTORY CORRELATES OF REPRODUCTIVE SPECIALIZATIONS

Some of the morphological correlates of the various reproductive behaviors of darters are discussed by Page & Swofford (1984). Life history characteristics also show trends correlated with reproductive specialization. Some trends are in the direction of r-selected characteristics, and some are in the direction of k-selected characteristics (MacArthur & Wilson 1967; Pianka 1978:122).

One dramatic trend accompanying the evolution of percids is to lay fewer, larger eggs (a k-selected trait). Species of *Stizostedion* lay up to 2,500,000 eggs (Filuk 1962) averaging 0.55–1.10 mm in diameter (Kryzhanovshy et al. 1953). Species of *Perca* lay up to 210,000 eggs averaging 1.0–2.1 mm (Thorpe 1977). Darters lay only up to a few thousand eggs averaging 0.7–2.7 mm (Page 1983:162). The largest eggs among percids are those of the highly evolved egg-clustering species in which parental care of the eggs warrants a large expenditure in the production of each egg.

Incubation periods seem to have changed little. *Stizostedion* and darters take about 25–30 days to hatch at 10°C and 8–10 days at 20°C (Marshall 1977; Page 1983:168).

In a more r-selected mode, advanced percids (darters) reproduce early (most at 1 year, a few at 2 years), whereas species of *Stizostedion* do not reach maturity until 2–6 years in the male and 3–6 years in the female (Marshall 1977). Longevity (r-selected) ranges from 20 years in *S. vitreum* (Scott & Crossman 1973:772) to only 1.5 years in several species of *Etheostoma* (Page 1983:169). Some of the most advanced species of darters have become semelparous; they mature at 1 year, reproduce, and die before a second spawning season (Page 1983:169). Semelparous species include egg attachers [*E. microperca* Jordan and Gilbert and *E. proeliare* (Hay)] and egg clusterers (*E. striatulum* Page and Braasch).

Some darters exist in large dense populations – to 33 individuals per square meter (Page 1983:170–171); the larger piscivorous percids exist in much smaller populations.

Decreasing body size (r-selected) has been a pervasive element of percid evolution and was discussed at length for darters by Page & Swofford 1984). In brief, darters feed on small benthic organisms and have become more efficient consumers by becoming smaller. Constraints on decreasing body size include living in gravel runs (correlated with egg burying); the smallest darters are pool inhabitants, including many egg-attaching and egg-clustering species. *S. vitreum* reaches a maximum length of about 107 cm and a maximum weight near 11.5 kg (Colby et al. 1979). Those values are 30 times the maximum length and 19,000 times the maximum weight of *E. fonticola* (Jordan and Gilbert), the smallest species of darter at a maximum length of 3.5 cm and weight of 0.6 g (Page & Burr 1979).

## SUMMARY

About one-fifth of all North America freshwater fishes are percids (the walleye, sauger, yellow perch, and 148 species of darters). In addition to being diverse, percids often occur in large populations and are important in determining the ecological characteristics of North American streams and lakes. Elsewhere percids occur only in temperate Eurasia (14 species). Knowing the reproductive requirements of these fishes is fundamental to understanding their positions in aquatic environments, protecting them, managing them, and predicting the impacts of proposed environmental alterations, such as impoundments and dredging.

Accompanying the evolution of a large diversity of percids has been the evolution of a variety of reproductive strategies. Among the 71 species of percids for which spawning behaviors are known, six types of behavior are recognized: broadcasting (including pit broadcasting), stranding, burying, attaching, clumping, and clustering (including alpha beta, and gamma clustering).

Broadcasting is the discharging of large numbers of eggs and sperm, usually over rocks or plants. It is the most primitive type of reproductive behavior among fishes and is characteristic of especially primitive percids (*Stizostedion vitreum*, *S. canadense*, and probably *S. marinum* and *Percarina demidoffi*). In pit broadcasting, found in *S. lucioperca*, eggs are broadcast over a pit constructed and guarded by the male.

Stranding is the unique habit of encasing eggs in long gelatinous strands. Stranding appears to be a derivative of broadcasting and is known in *Perca* and *Gymnocephalus*.

Burying is a derivative of, and is similar to, broadcasting, except that eggs are released just below rather than above the surface of the substrate. Among percids burying is restricted to darters. Among darters it is the primitive reproductive behavior and is known in 12 subgenera of *Percina* and *Etheostoma*.

Attaching behavior involves depositing eggs individually on plants or rocks over a wide area. It is derived from burying and, among percids, is known only in the genus *Etheostoma*. Attaching is found in at least nine subgenera and obviously has evolved independently several times.

Clumping is amassing eggs under a large stone, which subsequently is guarded by the male. It also is derived from burying but has evolved only within the subgenus *Nothonotus*. At present it is known in *E. maculatum*, *E. aquali*, and *E. microlepidum*.

Clustering is found in two unrelated subgenera, *Boleosoma* and *Catonotus*, of *Etheostoma*. It is a highly evolved derivation of attaching behavior in which eggs are concentrated in a single-layer cluster on the underside of a stone and are guarded by the male. Clustering evolved independently in *Boleosoma* and *Catonotus*.

Estimating the evolutionary history (phylogeny) of reproductive behaviors results in a better understanding of the relationships among percids. The phylogeny of breeding behaviors supports the contention that darters, the most primitive of which are buriers, are derivatives of, and among the species discussed here, probably the sister group of *Stizostedion*. A phylogenetic classification necessitates recognition of the subfamilies Etheostomatinae (containing the tribes Lucioperini, Etheostomatini, and Romanichthyini) and Percinae. The unique pigmentation of the first dorsal fin (bright red spots at the front and rear of the fin) of males of *Etheostoma sanguifluum* (Cope) and *E. aquali* Williams and Etnier is a synapomorphy indicating that the two are sister taxa. Thus, *E. sanguifluum* cannot remain a subspecies of *E. maculatum* Kirtland and is recognized here as a species. The subspecies known as *E. maculatum vulneratum* (Cope) becomes *E. sanguifluum vulneratum* (Cope).

Life-history correlates of reproductive specialization among percids include the production of fewer, larger eggs; earlier reproduction; semelparity; reduced longevity; denser populations; and reduced body size.

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# Wind Drift and Migration of Thrushes: a Telemetry Study

William W. Cochran and Charles G. Kjos

## ABSTRACT

Nocturnal migratory flights of four species of thrushes (*Catharus* spp.) that migrate through Illinois were investigated by radiotelemetry. Winds aloft were measured by theodolite and weather balloon during the birds' migratory flights. Analyses of the migratory flights of individual birds as they encountered different wind conditions indicated that individuals maintained a constant heading and airspeed regardless of the speed and direction of the wind, cloud cover, or landmarks. Lateral wind drift was mitigated and ground speed was maintained above about 6 m/s by the selection of flight altitudes where winds were more favorable. When winds were extremely unfavorable, birds landed. Path deviations caused by variable winds mask the remarkable ability of thrushes to maintain particular headings. Thus, unless winds are scrupulously accounted for, radiotelemetry, radar, and other observations of natural migration are of limited value in the study of orientation.

The spectacular nocturnal migrations of songbirds between breeding and wintering areas separated by many thousands of kilometers have inspired several decades of reseach that seem to have produced more questions than answers. A persistent question concerns how migrants respond to winds, particularly winds capable of blowing them off course, and another question concerns the effects of overcast skies. This paper is about how migrating thrushes (*Catharus* spp.) respond to wind and overcast skies.

Thorpe (1949) described a migratory journey as consisting of a start, a body, and a termination with each part representing different orientation problems for the migrant. The spring and fall destinations of thrushes passing through the area of this study were many hundreds to 1 or 2 thousand kilometers distant, and we consider the 200- to 700-km flights reported here representative of the "body" of thrush migrations. These flights were nocturnal, typically about 300 km in length, and usually separated by one or more nights without flight.

Allen (1939) pointed out that the motion of a bird over the ground is the sum of the bird's motion relative to the air and the motion of the air relative to the ground (wind). Although researchers have differed greatly about how birds react to winds, they have accepted the physical reality stated by Allen. The question has never been whether or not birds are affected by the wind but rather what, if anything, they do about it?

Data are presented for Swainson's thrushes [*C. ustulatus* (Nuttall)], veeries [*C. fuscescens* (Stephens)], gray-cheeked thrushes [*C. minimus* (Lafresnaye)], and hermit thrushes [*C. guttatus* (Pallas)]. Graber et al. (1971) delineate the wintering and breeding ranges of these species as well as their occurrence and

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progress through Illinois during migration.

## METHODS

Radio-tagged thrushes were followed by means of direction-finding equipment carried in an automobile. Approximations of the thrushes' flight paths were obtained by plotting on U.S. Geological Survey maps (scale 1:250,000) the places and times where thrushes crossed roads. We refer to a line between two plotted road crossings as a *track segment,* the azimuth of a track segment as a *track direction*, the distance represented by a track segment divided by the time difference between two plotted road crossings as a *track segment,* and azimuth of a track segment as a *track direction,* the distance represented by a track segment divided by the time difference between its end points as a *track speed,* and the track direction and speed collectively as the *track vector.* Two or more connected track segments are *estimated flight vector.* Where we refer to the actual path of a bird we use *course,* ground speed, and *path vector* as counterparts to track direction, track speed, and track vector, respectively. Where we refer to actual bird performance, the terms *heading, airspeed,* and *flight vector* are used without qualifying them as estimated. Some authors have used *track* to describe the direction of a path, but the correct word is *course.* Therefore, to avoid confusion, we have substituted *path approximation* in those cases where *track* could properly have been used as a noun. Directions are given in degrees, clockwise from true north. Altitudes are referenced to the earth's surface. Times are central standard.

When referring to the behavior of individual thrushes, we often use the term *preferred heading* as a short and convenient substitute for the *mean of a tightly clustered set of measured headings.* In addition, *preferred* implies something special about the direction. Although we do not speculate on what is special, the preferred headings of thrushes always pointed toward some part of the breeding or wintering area of the species (as seasonally appropriate), but not always away from the wintering area from which an individual could have been coming. Others have used the term similarly to describe the means of sets of headings (usually of different individuals) without implying that particular goals (such as nesting sites) were in the mean direction.

The methods used to determine the geographic (road crossing) points, which define track segments, and to measure or estimate bird altitudes are discussed in the Appendix. Four different methods were used to estimate the headings corresponding to track segments. Occasionally two of the methods were used to estimate a heading for a single track segment. For an extensive discussion of these methods, described briefly below, refer to the Appendix.

Of the 71 heading (and airspeed) estimates in Table 1, 40 were obtained by constructing vector triangles in which an estimated flight vector was the vector difference between the track vector and wind vector. Estimated headings obtained with this method are referred to as *calculated heading estimates.* The method required knowledge of the birds' altitudes and the winds at the birds' altitudes. Winds were measured over increments of altitude. Therefore, the altitude of a bird was required. This method also provides an airspeed estimate.

Six heading estimates were made by the departure method. During the first 100 or so seconds of flight, thrushes climbed through winds from tree level to no more than 150 m altitude. Also, during the period after sunset when migratory flights usually began, the measured winds from surface to 150 m were sometimes light. The departure method is actually a special case of the more general vector triangle method but with a small crosswind component. Therefore, measurement of the initial track direction and confirmation of light crosswinds are required. The initial track direction with a small allowance for crosswind provided an estimated heading. One way by which the track direction was measured was to determine the place where a bird crossed over a road within about 2 km of the starting point. The potentially higher track direction error associated with the short track segment was offset by a higher accuracy of the plotted points, i.e., the departure point was known to within 10–20 m and the crossover point could be determined to within 30–40 m due to the low bird altitude and the reduction of map errors through adequate preparation.

Nineteen heading estimates were determined by the head-null method. This method required measurement of the azimuth of the null plane of the transmitter antenna radiation pattern. In the transmitter attachment method used in this study (Cochran 1972) and in a better method (Raim 1978), the transmitter is mounted on a bird's back, centered between the points where the wings attach to its body (Fig. 1). The 30-cm × 0.013-mm wire antenna exits the transmitter flush with a bird's back and extends backwards over and beyond the tail. When a bird is in flight, the antenna and the bird's heading are both in the same vertical plane and the antenna is approximately horizontal. No horizontally polarized energy (radio waves) is radiated in this plane. In practice, this arrangement caused the signal to fade completely and then return as the tracking vehicle was driven on a road which passed through this plane. The azimuth of the plane (the bird's heading) was bounded by the azimuth of the last bearing taken as the signal faded and the first taken when the signal returned.

The six remaining heading estimates were made using the cross-polarization method, which required the observer to be positioned approximately under a bird. A receiving antenna pointed up at the bird gave the maximum signal when the antenna elements were aligned parallel with the transmitting antenna and zero signal (a null) when at right angles (cross polarized) to the transmitting antenna. Ranges to overhead birds were equal to their altitudes and thus, never greater than a few kilometers. At such short distances signal maxima were strong and the nulls sharp. When a signal was nulled, the azimuth of the receiving antenna elements was at right angles to the transmitter antenna with the latter in the same plane as the bird's heading, as described above for the head-null method.

Both the head-null and cross-polarization methods resulted in measurements with a 180° ambiguity, because a bird may be headed in either of two azimuths which define the same plane. To resolve the ambiguity, we made flight vector estimates by calculation from the track vector and wind vectors at all conceivable bird altitudes.

## Transmitter Bias

It is axiomatic that the weight of the transmitter (approximately 6 percent of a thrush's body weight) affected the flight of the birds we followed, but we do not know whether the effect was faster-than-normal airspeeds (at normal angles of attack with higher-than-normal energy use), normal airspeeds (at higher-than-normal angles of attack and energy use), or slower-than-normal airspeeds (at higher-than-normal angles of attack and normal energy use). The fore-aft centering of the transmitter may have determined which of these effects pertained. We tried to attach each transmitter with its center as near as possible to the places where a bird's wings attach to its body, but in practice the looseness of a thrush's skin and the way in which the bird was held during attachment sometimes resulted in an attachment that was slightly forward of the desired spot. Some of the variability in the airspeeds reported in this paper may have been due to variations in transmitter placement.

The mean of the 17-airspeed sample of Cochran et al. (1967) was 13.1 m/s. Calculations for most of those samples were made from plots on highway maps, which later were found to have a 7-percent scale error. Adjustment for this error brings their mean airspeed down to about 12.2 m/s, but this is still 20 percent higher than the 10.1 m/s mean for the airspeed estimates we now report. A species-by-species comparison between the two studies shows the mean airspeeds of Cochran et al. (1967) to be higher by 16, 39, and 25 percent for Swainson's, veery, and gray-cheeked

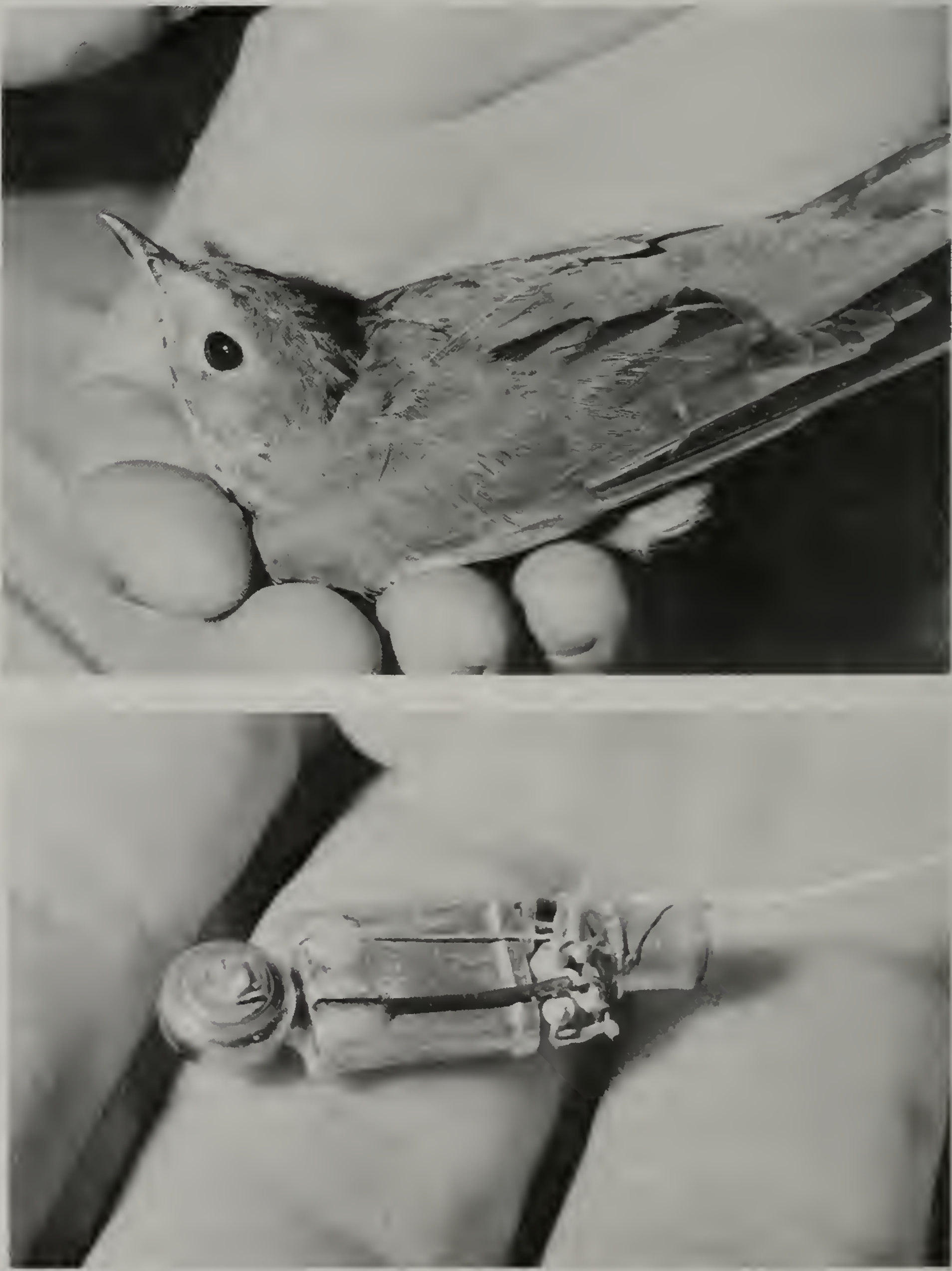


Fig. 1. – (Above) Swainson's thrush carrying a 1.3-g radio transmitter of the type currently in use (Cochran 1980). (Below) a 2.2-g transmitter of the type used in the study reported in this paper.

thrushes, respectively. Therefore, the airspeed difference cannot be attributed to a difference in species mix in the two studies. Most of the birds in this study were fitted with 2.2- to 2.4-g transmitters by C. Kjos, whereas in the study by Cochran et al. (1967), 2.6- to 2.8-g transmitter attachments were about equally divided among R. Graber, W. Cochran, and G. Montgomery. A consistent difference in fore-aft centering of the transmitter is one explanation for the difference between the mean airspeed from the two studies. However, it seems more likely that the heavier transmitters in the earlier study required birds to fly slightly faster to provide additional lift.

Although we believe that thrushes' airspeeds are affected by the attachment of transmitters and that radiotelemetry is not ideal for studying absolute airspeed, the speed analyses in this paper are directed toward finding whether thrushes change their airspeed, altitude, and course direction in response to changes in wind and not toward finding how fast they fly. Analyses of responses to changes in wind are unaffected by the bias discussed above.

It is possible that transmitter attachment left or right of a bird's center of gravity affects the direction of flight. We were more successful in left-right centering of transmitters than we were in fore-aft centering. Furthermore, our analyses are concerned with changes or lack of changes in direction of flight in relation to wind. Therefore, we do not believe that variations in transmitter attachment could have affected our analyses.

The question of the effect of a transmitter, no matter how well centered, on the orientation mechanisms involved in migration is one which we cannot address directly. The migratory flights we observed were within the broad limits of what is generally accepted as normal with regard to progress and orientation toward the breeding or wintering areas. As we will show, the thrush migrations we observed were, with few exceptions, characterized by headings that were nearly constant regardless of the direction or speed of the wind or the presence or absence of cloud cover. We cannot conceive of how a transmitter could impart to a bird the urge or ability to maintain a particular heading under a variety of wind conditions while depriving it of an urge or ability to behave in some other way.

## SUPPLEMENT TO RESULTS OF THE 1965–1966 STUDY (Cochran et al. 1967)

We will first review and discuss the flights of two thrushes reported in Cochran et al. (1967). Although the authors of that paper provided maps showing path approximations, some of which were crooked enough to preclude significant compensation for wind, they did not materially discuss wind drift. The flight numbering they used is retained here, and the path approximations for the two thrushes are shown in their Fig. 7.

For Swainson's #5, Cochran et al. (1967:Table 1) gave only average values for heading estimates and track directions. Detailed data are given here. This Swainson's passed the airport at Springfield, Illinois, when and where winds aloft were being measured by the U.S. Weather Bureau. Several measurements of the bird's altitude and location were made, and from these and the winds-aloft data we calculated estimated headings (±10°) and estimated airspeeds (m/s shown in parentheses) of 295°(10.5), 298°(12.9), and 305°(12.4) for track directions and speeds of 220°(9.5), 252°(7.8), and 286°(7.4), respectively. The sky was clear for this entire flight.

The next evening was completely overcast, and the bird was tracked for 83 minutes after it took off. The heading was estimated at 309° (±10°) for a track direction of 302°. The spread of estimated headings for this thrush (295°-309°) was 14°, less than one-fourth the 82° spread in track directions.

That a single heading, 300°, was within the error range of all estimated headings, that all estimated headings pointed to the breeding range of the species, and that at least one track direction, 220°, pointed well outside the breeding range are consistent with constant-heading behavior. If the differences in estimated headings were not due to measurement errors, it is noteworthy that the greater the deviation of a track direction from a 300° preferred heading, the greater also the deviation of the corresponding estimated heading from 300°. Instead of altering heading to compensate partially for wind drift, this Swainson's may have flown headings which actually increased drift. However, looked at another way, the indicated clockwise heading shifts (295° to 298° to 305°) may have resulted from a slowly altered heading in response to, and to compensate for, the counterclockwise drift in track directions (up to 80°) earlier in the flight.

Cochran et al. (1967:222) mentioned a curvature in the flight path of gray cheek #19. They stated that the change occurred under clear skies but did not elaborate. Detailed data are given here. A 111-minute track segment was in a direction of 314° at a ground speed of 15.8 m/s and was within 35 km of the Peoria, Illinois, airport when winds were being measured there. The altitude of the bird was between 300 and 1,300 m during this segment. Depending on the altitude assumed, estimates varied from 332° to 342° for heading and from 11.3 to 10.1 m/s for airspeed. Later, during the last 53 minutes of the flight, the altitude was between 100 and 300 m with a track direction of 358° and a ground speed of 18 m/s. This portion of the flight was not well situated relative to the schedules and locations of U.S. Weather Bureau winds-aloft measuring stations. Fortunately, there were no frontal systems in the area, and the temporal and spatial variations in wind measured at the various reporting stations followed a consistent pattern, allowing the use of the 2315 CST winds measured at Madison, Wisconsin, about 65 km from the flight. The heading and airspeed estimates were 338° at 10.7 m/s and 348° at 11.5 m/s for altitudes of 300 and 150 m, respectively. Whereas between the earlier and last parts of the flight the track direction shifted 44°, the heading estimates changed less than 17°, and the heading appeared to have been consistent in a direction of 338°-342°.

The data indicate that as the wind direction shifted clockwise, the heading may have shifted clockwise also. A clockwise heading change, opposite to that which would produce compensation for wind drift, could be called negative compensation. One special case of negative compensation is orientation at a fixed angle to the wind, as suggested by Vleugel (1962). Another special case is downwind orientation as reported by Gauthreaux & Able (1970). Gray-cheeked thrush #19 did not fly downwind nor did it fly a constant angle to the wind, a 100° clockwise shift in winds being associated with only 5° heading change, if any.

Paradoxically, the indicated 5° clockwise heading shift (337° to 342°) may have resulted from a slowly altered heading in response to the early counterclockwise drift (track direction = 314°). This case illustrates, as did the data for Swainson's #5, how the same data may be interpreted as partial negative (instantaneous) compensation behavior or as positive compensation behavior achieved by a slow response.

## RESULTS, 1967–1972, ON EFFECTS OF WIND

The flights of 36 thrushes were reviewed in a process of selecting the 14 for which data are presented in Table 1. Of the 22 that were excluded, either winds did not vary significantly during

Table 1. — Estimated heading, airspeed, and altitude for 65 selected track segments of migrating thrushes, 1968 — 1972.

| Species,[a] Year, Number[b] | Date | Time[c] (CST) | Dur.[c] (min) | Location[d] Lat. | Location[d] Long. | Altitude[e] Min Max (meters) | Track Direction (degrees) (Track Speed) (m/s) | Estimated Heading (degrees) (EAS)[f] (m/s) | Error[g] (± degrees) | Sky[h] | MT[i] | MH[j] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sw6809 | 09/30 | 2200 | 1 | 40° 7.0′ | 88°17.0′ | <30 | 150( D ) | 155( D ) | 5 | C | 131.0 | 155.0 |
| | | 2235 | 19 | 40°11.5′ | 87°54.0′ | 200 – 300 | 075(15.2) | 157( 9.8) | 10 | C | | |
| | | | | | | | | 150(HN) | | C | | |
| | | 2257 | Landed | | | | | | | | | |
| | 10/03 | 1830 | 25 | 40°13.6′ | 87°46.7′ | 100 – 500 | 168(20 ) | 160(10 ) | 10 | C | | |
| He6810 | 09/29 | 2010 | 5 | 40° 7.0′ | 88°17.0′ | <50 | 135( ? ) | 135( ? ) | 5 | C | 093.7 | 141.0 |
| | 10/01 | 2137 | 38 | 40° 5.9′ | 88°15.2′ | 300 – 500 | 052(22 ) | 143(HN) | 4 | C | | |
| | | 2347 | 40 | 40°18 | 86°16.0′ | 100 – 300 | 094(24 ) | 145(HN) | 6 | C | | |
| | 10/02 | 0027 | Landed | | | | | | | | | |
| Ve6901 | 05/03 | 2035 | 22 | 40° 7.0′ | 88°17.0′ | 20 – 300 | 035(18.2) | 018( 8.1) | 6 | C | 63 | 62.3 |
| | | 2130 | 11 | 40°28.0′ | 87°47.9′ | 550 – 600 | 056(17.2) | 052(13.5) | 10 | C | | |
| | | 2240 | 15 | 40°45.0′ | 87° 2.6′ | 550 – 600 | 071(16.5) | 089(14.5) | 5 | C | | |
| | | 2355 | ? | 40°47.7′ | 86°52.3′ | <500 | 090( ? ) | 090(HN) | 5 | C | | |
| Sw6902 | 05/05 | 2353 | 1 | 40° 7.0′ | 88°17.0′ | <30 | 295( D ) | 295( D ) | 3 | C | 302.7 | 291.7 |
| | 05/06 | 0000 | 11 | 40° 8.0′ | 88°20.1′ | 450 – 550 | 315(14.5) | 292( 9.5) | 4 | C | | |
| | | 0128 | 30 | 40°16.4′ | 88°33.1′ | 150 – 200 | 298(13.7) | 288( 8.1) | 3 | C | | |
| Sw6905 | 05/23 | 2023 | 13 | 40° 7.0′ | 88°17.0′ | 20 – 300 | 268( 9.5) | 290( 9.0) | 5 | C | 299.8 | 295.1 |
| | | 2036 | 58 | 40° 6.5′ | 88°22.4′ | 300 – 800 | 275( 9.8) | 293( 9.4) | 4 | C | | |
| | | 2134 | 82 | 40° 8.8′ | 88°45.0′ | 800 –1050 | 294( 8.0) | 299( 9.4) | 4 | C | | |
| | | | | | | | | 295(HN) | 4 | | | |
| | | 2256 | 46 | 40°17.4′ | 89°10.1′ | 250 – 950 | 278( 5.8) | 295(HN) | 6 | C | | |
| | 05/24 | 0037 | 80 | 40°33.2′ | 89°49.3′ | 200 – 500 | 320( 6.7) | 300(11.5) | 5 | C | | |
| | | 0157 | 83 | 40°52.1′ | 90° 2.6′ | <100 | 301( 8.0) | 289(12.5) | 7 | C | | |
| | | 2106 | 40 | 40°55.9′ | 90°34.7′ | 1800–2500 | 254( 8.0) | 301( 7.5) | 5 | C | | |
| | | 2233 | 47 | 40°54.0′ | 91° 8.0′ | 150 – 300 | 352( 8.9) | 298( 9.5) | 12 | C | | |
| | | 2320 | 73 | 41° 6.1′ | 91°11.3′ | 100 – 150 | 335(11.2) | 292(10.5) | 10 | C | | |
| | 05/25 | 0224 | 72 | 41°58.3′ | 91°48.4′ | <100 | 321(10.7) | 301(12.4) | 6 | C | | |
| | | | | | | | | 295(HN) | 6 | | | |

Table 1. — Continued

| Species,[a] Year, Number[b] | Date | Time[c] (CST) | Dur.[c] (min) | Location[d] |  | Altitude[e] Min Max (meters) | Track Direction (degrees) (Track Speed) (m/s) | Estimated Heading (degrees) (EAS)[f] (m/s) | Error[g] (± degrees) | Sky[h] | MT[i] | MH[j] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  | Lat. | Long. |  |  |  |  |  |  |  |
| Gc7003 | 05/08 | 1955 | 88 | 29°13.0′ | 89°14.1′ | 250 – 350 | 350(15.0) | 012( 9.0) | 7 | C | 004.0 | 011.0 |
|  |  | 2208 | 188 | 30°18.8′ | 89°17.7′ | 100 – 150 | 018(16.0) | 010( 9.0) | 8 | C |  |  |
| Sw7005 | 05/19 | 2052 | 49 | 40°29.7′ | 88°21.0′ | 100 – 300 | 352(14.4) | 330(HN) | 5 | C | 341.0 | 332.6 |
|  |  | 2210 | 55 | 40°53.3′ | 88°33.4′ | 200 – 250 | 343( 9.7) | 326( 9.8) | 4 | C |  |  |
|  |  | 2305 | 50 | 41° 9.5′ | 88°39.2′ | 150 – 200 | 353(10.5) | 332( 9.5) | 3 | C |  |  |
|  |  | 2355 | 40 | 41°26.5′ | 88°42.2′ | 200 – 250 | 353( 9.1) | 334( 8.8) | 4 | C |  |  |
|  |  |  |  |  |  |  |  | 340(HN) | 6 |  |  |  |
|  | 05/20 | 0035 | 67 | 41°37.8′ | 88°44.3′ | 250 – 300 | 323(15.1) | 335(12.6) | 6 | C |  |  |
|  |  |  |  |  |  |  |  | 340(HN) | 6 |  |  |  |
|  |  | 0237 | 64 | 42°35.1′ | 89°39.3′ | 200 – 250 | 322(18.3) | 333(11.4) | 3 | C |  |  |
| Ve7008 | 05/21 | 2335 | 49 | 40° 7.0′ | 88°17.0′ | 100 – 200 | 025(10.9) | 352( 9.5) | 5 | C | 002.6 | 352.0 |
|  | 05/22 | 2025 | 38 | 40°22.8′ | 88° 8.0′ | 500 – 700 | 017(19.8) | 358(10.0) | 6 | C |  |  |
|  |  | 2223 | 17 | 41°15.8′ | 87°49.5′ | 250 – 350 | 008(10.6) | 350( 8.1) | 6 | C-O |  |  |
|  | 05/23 | 0023 | 15 | 41°54.8′ | 87°50.5′ | <200 | 305( 7.0) | 315( 8.0) | 6 | O |  |  |
|  |  | 0038 | Landed in rainstorm |  |  |  |  |  |  |  |  |  |
|  | 05/28 | 2011 | 1 | 41°56.0′ | 87°54.5′ | <30 | 350( D ) | 350( D ) | 3 | C |  |  |
|  |  | 2025 | 123 | 42° 3.0′ | 87°57.0′ | 600 –1500 | 333(23.0) | 350(10.0) | 10 | C |  |  |
|  |  |  |  |  |  |  |  | 355(HN) | 4 |  |  |  |
| Sw7012 | 09/24 | 2033 | 5 | 40° 7.9′ | 88° 8.1′ | 200 – 500 | 083(14.6) | 150(HN) | 4 | O | 107.4 | 150.2 |
|  |  | 2043 | 8 | 40° 8.0′ | 88° 4.8′ | 600 – 700 | 090(14.4) | 148( 8.4) | 5 | O |  |  |
|  |  | 2051 | 44 | 40° 8.0′ | 87°59.0′ | 500 – 600 | 097(14.0) | 150(10.6) | 5 | O |  |  |
|  |  | 2238 | 58 | 39°46.0′ | 87°14.0′ | 30 – 100 | 142( 9.5) | 153( 9.7) | 4 | O |  |  |
|  | 09/25 | 0032 | 116 | 39°11.0′ | 86°32.0′ | 150 – 200 | 125( 9.8) | 150( 8.1) | 6 | O |  |  |
| He7015 | 10/24 | 1935 | 1 | 40° 8.3′ | 88° 8.1′ | <30 | 190( D ) | 190( D ) | 3 | O | 213.2 | 189.2 |
|  |  | 1950 | 24 | 40° 5.4′ | 88°12.1′ | 150 – 250 | 228( 9.2) | 190(10.4) | 5 | O |  |  |
|  |  | 2017 | 10 | 39°59.7′ | 88°20.4′ | 300 – 450 | 245(12.2) | 192( 9.8) | 6 | O |  |  |
|  |  | 2100 | 85 | 39°47.3′ | 88°33.1′ | 100 – 200 | 213( 7.1) | 189( 9.0) | 3 | O-C |  |  |
|  |  | 2240 | 6 | 39°28.0′ | 88°47.2′ | <50 | 190(10.0) | 185(HN) | 4 | O |  |  |

Table 1 — Continued

| Species,[a] Year, Number[b] | Date | Time[c] (CST) | Dur.[c] (min) | Location[d] |  | Altitude[e] Min Max (meters) | Track Direction (degrees) (Track Speed) (m/s) | Estimated Heading (degrees) (EAS)[f] (m/s) | Error[g] (± degrees) | Sky[h] | MT[i] | MH[j] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  | Lat. | Long. |  |  |  |  |  |  |  |
| He7018 | 10/28 | 1901 | 9 | 40° 8.3′ | 88° 8.1′ | 100 – 200 | 165( 9.0) | 190( 8.0) | 5 | O | 185.7 | 193.0 |
|  |  | 2002 | 24 | 39°47.5′ | 88°10.9′ | 500 –1500 | 202(13.5) | 193(HN) | 5 | O |  |  |
|  |  | 2050 | 47 | 39°29.6′ | 88°18.0′ | 1000–2000 | 190(13.2) | 196(CP) | 4 | O |  |  |
| Ve7103 | 05/08 | 1955 | 39 | 40° 7.0′ | 88°17.0′ | 250 – 350 | 346( 9.7) | 317(10.1) | 5 | C | 352.0 | 318.3 |
|  |  | 2058 | 40 | 40°27.3′ | 88°21.8′ | 200 – 400 | 000(13.8) | 320(HN) | 4 | C-O |  |  |
|  |  | 2204 | 9 | 40°50.0′ | 88°20.0′ | <150 | 210(19.0) | (210<head<270) |  | O |  |  |
|  |  | 2213 | Landed in rainstorm |  |  |  |  |  |  |  |  |  |
|  | 05/10 | 2012 | 47 | 41° 5.7′ | 88°34.0′ | >1300 | 009(16.3) | 320(HN) | 4 | C |  |  |
|  |  | 2059 | 55 | 41°31.0′ | 88°29.9′ | <1000 | 333(17.9) | 316(HN) | 5 | C |  |  |
| Sw7118 | 05/29 | 1958 | 2 | 40° 8.4′ | 88° 8.1′ | <100 | 343( D ) | 343( D ) | 5 | C | 332.0 | 339.7 |
|  |  | 2048 | 65 | 40°27.6′ | 88°30.5′ | 2000–2500 | 318(11.2) | 345(HN) | 4 | C |  |  |
|  |  | 2325 | 80 | 41° 7.4′ | 89°12.1′ | 1500–1800 | 335(10.4) | 341( 9.8) | 5 | C |  |  |
|  | 05/30 | 0306 | 38 | 42°13.7′ | 89°49.5′ | 150 – 300 | 355(10.6) | 336( 9.0) | 6 | C |  |  |
|  |  | 2120 | 90 | 43° 9.8′ | 90°41.8′ | 1000–2000 | 331(16.3) | 338(CP) | 6 | C |  |  |
|  | 05/31 | 0126 | 68 | 44°34.3′ | 91°28.5′ | 1000–1500 | 356(15.0) | 335(CP) | 4 | C-O-C |  |  |
|  |  | 0350 | 8 | 46° 0.0′ | 92° 3.0′ | <200 | 286( ? ) | 340(CP) | 6 | C |  |  |
| Gc7207 | 05/16 | 2005 | 26 | 40° 1.3′ | 88°15.1′ | 100 –1000 | 312(11.3) | 348(CP) | 4 | C | 338.3 | 352.0 |
|  |  | 2130 | 36 | 40°29.1′ | 88°39.2′ | 200 – 500 | 345(12.6) | 353(CP) | 4 | C |  |  |
|  | 05/17 | 0050 | 32 | 41°46.2′ | 88°51.5′ | <100 | 358( 9.4) | 355(HN) | 6 | C |  |  |

[a] Letters identify species as veery (Ve), gray cheek (Gc), hermit (He), or Swainson's thrush (Sw).

[b] Year is year of flight and number is an identification number.

[c] Time refers to start (CST) and Dur. to the duration (minutes) of track segment.

[d] Location refers to the start of the track segment.

[e] Altitude is given in meters above earth's surface.

[f] EAS is estimated air speed in meters per second; accuracy is typically ±5 percent, or identifies a method which does not yield airspeed, i.e., heading null (HN), cross-polarization (CP), and departure (D) methods.

[g] Error refers to estimated heading.

[h] Sky refers to cloud cover during track segment:
C (clear or partly cloudy) and 0 (100 percent cloud).

[i] MT is mean of track segments.

[j] MH is mean of estimated headings.

the period of observation, or wind measurements were not available sufficiently near the flight path to permit analyses (e.g., see Fig. 2). For the 14 selected thrushes, track direction data were available for flight in winds differing significantly (1) during a single night's flight, (2) between different nights, or (3) during ascent or descent. From the numerous track segments measured for each of the 14 individuals, we selected (for analysis and presentation)

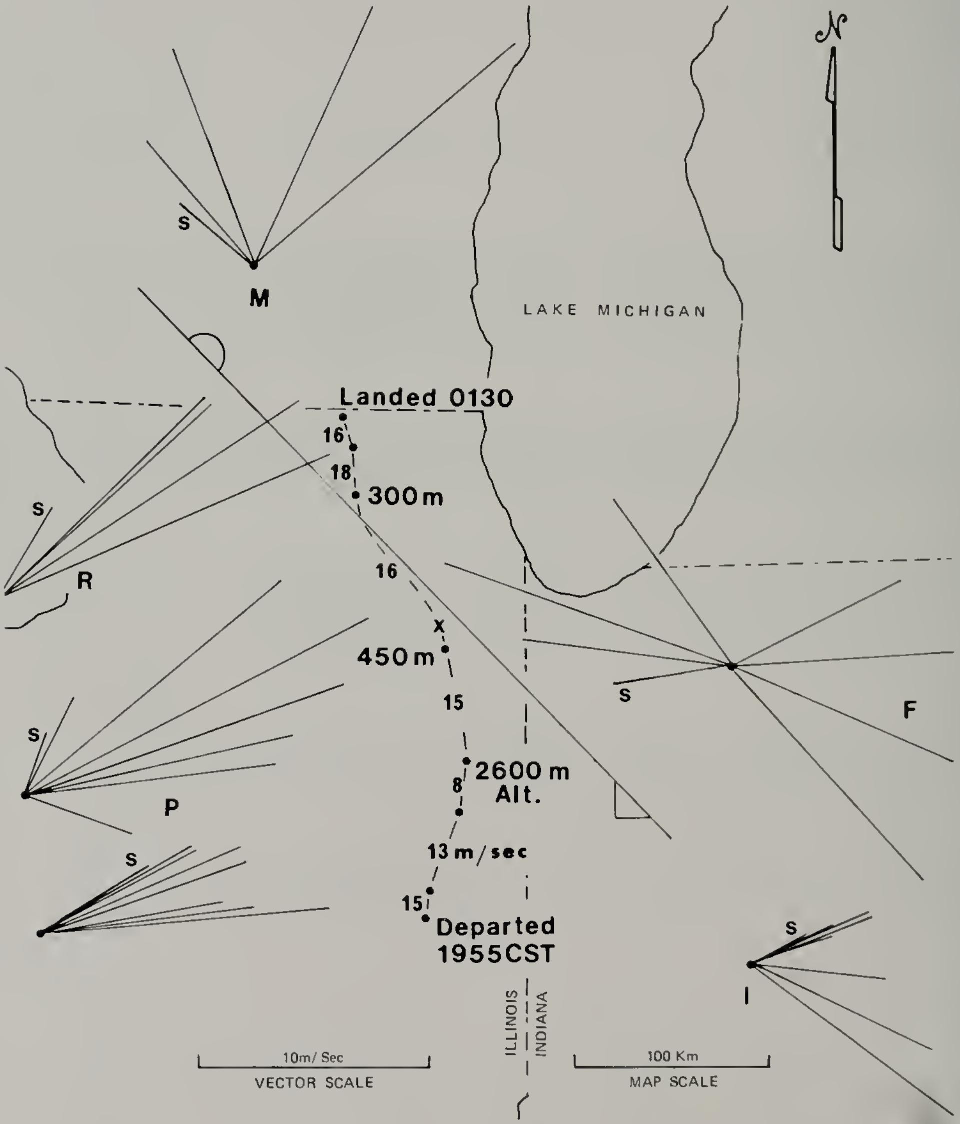


Fig. 2. – Track of veery 6705, area winds aloft, and the position of a weak front. Winds-aloft data are by the U.S. Weather Bureau (USWB) for 2315 CST, 25 May 1967, except for P, where the lower set of winds is for 1730 CST. Letters P, R, M, F, and I are the geographic locations of the places where the USWB measured winds aloft (drawn nearby). Winds are for increasing altitudes, going clockwise from surface wind (marked S) to 150, 300, 800, 1,300, 1,800, 2,300, and 2,800 m. The position of the front was taken from the USWB surface chart for midnight, 25 May. Track speeds (one- or two-digit numbers between points marking the bird's path) were computed from straight-line distances between points. Bird altitudes shown are ±20 percent. X is the position of the bird at 2315 CST and also the approximate position of the warm front at that time.

segments for which headings could be estimated with minimal error by vector subtraction of winds aloft measured close to the bird's paths and near their altitudes or by the head-null or cross-polarization methods.

Track directions and heading estimates for each individual bird were normalized about their respective means so that the data for all birds (Table 1) could be pooled to examine the relationship between courses and headings (Fig. 3). When the use of two methods resulted in two heading estimates for a single track direction, as indicated by a double entry in the heading estimate column in Table 1, the mean of the two estimates was used in constructing Fig. 3.

Course-heading plots are useful, because constant-course (complete compensation for wind) and constant-heading (no compensation for wind) behaviors, in variable crosswinds, would produce distributions along the vertical and horizontal axes, respectively. Distributions representing headings which partially compensate for lateral wind drift, or which are at a constant nonzero angle to the wind, are difficult to interpret in course-heading plots. However, the point is moot for the thrush data, because heading estimates are distributed along the horizontal axis.

The actual data do not consist of courses and headings but of approximations to these, namely, track directions and heading estimates. For simplicity, track direction versus heading estimate plots (e.g., Fig. 3) will be called TD-HE plots. Track directions were better estimates of courses (±1° or 2°) than heading estimates were of headings (±3°-10°). This fact biases against track variations the impression given by a TD-HE distribution unless the variations are significantly greater than the error range of heading estimates. It is for this reason that flights were excluded from the analysis, as mentioned above, if wind variations were too small to alter courses by an amount greater than the probable error range in estimated headings.

The other consequence of the 6°-20° error range in heading estimates is that small heading changes, whether in response to wind or for other reasons, are masked. Some of the vertical scatter of points in the TD-HE plot (Fig. 3) may thus represent real heading changes which are small compared with corresponding variations in track directions.

## Swainson's Thrush 6905 — An Example

The flight of Swainson's 6905 was chosen as an example for discussion because it was observed flying in winds which varied from night to night, during the same night, and significantly and rapidly with altitude on one night. Track directions and heading estimates for this bird are distinguished by a separate symbol in Fig. 3.

Swainson's 6905 was netted at 1130 on 15 May in a 0.5-ha woods located on the west edge of Champaign, Illinois. It weighed 36.7 g. A 2.4-g transmitter was attached, and the bird was released within 25 minutes of its striking the net. It remained in the woods until the evening of 23 May, when it departed on a flight which ended the next morning in a park near the center of Galesburg, Illinois. It departed that evening, flew all night, and landed at twilight in a 40-ha woodlot about 18 km southeast of Waterloo, Iowa, where it was renetted on the same morning for the purpose of replacing the transmitter with one having a fresh battery. It weighed 34.7 g, not including the transmitter weight. The transmitter was not replaced, because the adhesive held it so firmly that the bird might have been wounded had the transmitter been pulled off. The bird was released in the woodlot and was monitored in the woodlot until the battery failed 2 days later.

The heading estimates for track segments T1, T2, and T3 (Fig. 4) show a progressive clockwise shift totaling 9° into winds coming from the bird's right side. Similarly, the heading estimates for T4 and T5 indicate an 11°

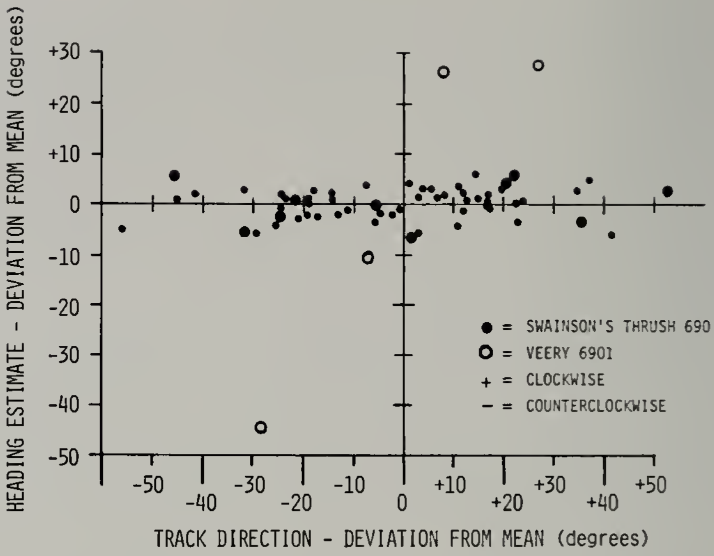


Fig. 3. – Plot of deviations of track directions and estimated headings, for individual thrushes, from the respective mean value of track direction and etimated heading. Data are from Table 1.

counterclockwise shift into winds with a component coming from the bird's left side. Also, the airspeed estimate for T5 was greater than that for T4. These changes are consistent with a compensatory response to lateral wind drift by a gradually altered heading and airspeed or by partial negative compensation.

During the first 40 minutes of the second night's flight (Fig. 5) the track direction changed by more than 90°. The bird departed while we measured winds aloft 5 km west of the bird. The first two bearings to the bird were taken from this place 1 and 5 minutes after the bird took off. Subsequently, seven additional bearings were taken as the tracking vehicle was driven on a circuitous route under and around the path of the bird. These bearings, and the times and places from which they were taken, are shown on the maps of Fig. 6. Although bearings were taken continually, only those above, taken carefully while the vehicle was stopped at known map points, could be used for analysis. Between 21 and 26 minutes after the bird's takeoff, while stopped, we made repeated attempts to measure the elevation angle to the bird but failed because the angle was below 30°, where ground reflections cause erratic readings.

The series of bearings and the times, coupled with the winds measured in the same airspace as the bird, provided data for evaluation of computer simulated paths of a bird's hypothetical constant-heading, constant-airspeed ascent through the winds aloft that we measured. The process was iterative, a matter of computingpaths for different headings, airspeeds, and ascent rates and noting which combination best fit the observed bearing-time data. Sixty iterations revealed that a 290° heading, 8.1-m/s airspeed, and 0.66-m/s ascent rate fit all bearing-time data within 5 percent. Fig. 6A, 6B, and 6C illustrate that headings of 280° and 300°, airspeeds of 7.2 and 9.0 m/s, and ascent rates of 0.56 and 0.81 m/s, respectively, cause poor fits to the bearing-time data.

To understand this analysis, it is important to note that there is no guarantee, no matter how many parameter combinations are tried, that a particular model will produce a path that will match (fit) the bearing-time data. If we had tried all combinations of headings, airspeeds, and ascent rates in increments of 1°, 0.1 m/s, and 0.01 m/s, respectively, and had found none which, with the constant parameter model, produced a path which nearly

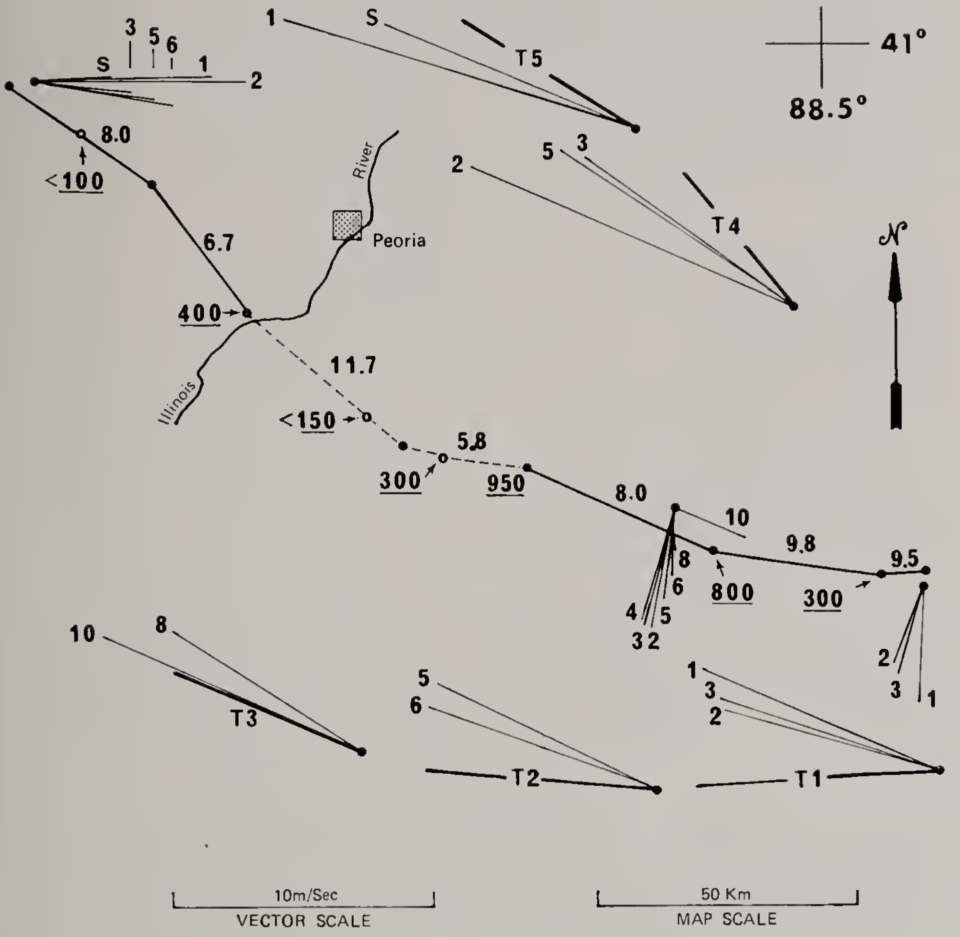


Fig. 4. – The approximate 23–24 May path of Swainson's 6905, winds aloft vectors measured along the path (shown near where measured), and vector representation of estimated headings (light lines) and track vectors (heavy lines with "T" designators). Track speeds (numbers along lines connecting solid points) are in meters per second for the straight-line distance between points. Bird altitude measurements (underlined) are in meters above the surface and are accurate to ±20 percent, or better. Vector plots are for track segments drawn as solid lines and are labelled chronologically T1, T2, etc. Winds-aloft vectors are labelled with altitude in 100's of meters (S = surface). Each estimated heading in the vector plots (light lines) is labelled with the altitude (in 100's of meters) of the wind used for its computation, and corresponding wind vectors are shown to the same scale separately with the wind vector sets. T1 and winds taken at departure go together, estimated heading vectors shown for T2 and T3 are from the second set of winds, taken along the path, and the vectors for T4 and T5 use the last set of winds, taken just after the bird landed.

fit the observed directions and times, we would have been required to reject the model, our bearing-time data, our wind data, or some or all of these. Similarly, had the model provided a fit only for unbelievable parameters, e.g., an airspeed of 40 m/s, a rejection would have been required. We could then have constructed more complicated behavioral models ad nauseum in hopes of finding one which fit the bearing-time-wind data. That the simplest model (constant behavior, i.e., constant heading, airspeed, ascent) produced a path consistent with our bearing-time-wind data and that the airspeed, heading, and ascent rate required to produce the fit were close to those observed for this bird in other portions of its migration, constitute powerful support for both model and parameters. Of course, there are numerous other models, involving variable parameters, which can produce fits to our bearing-time-wind data, but we reject these on grounds of simplicity in hypothesis (Barker 1957: Chapter 5).

Later in the flight, as the bird descended in the vicinity of the Mississippi River, the track direction again

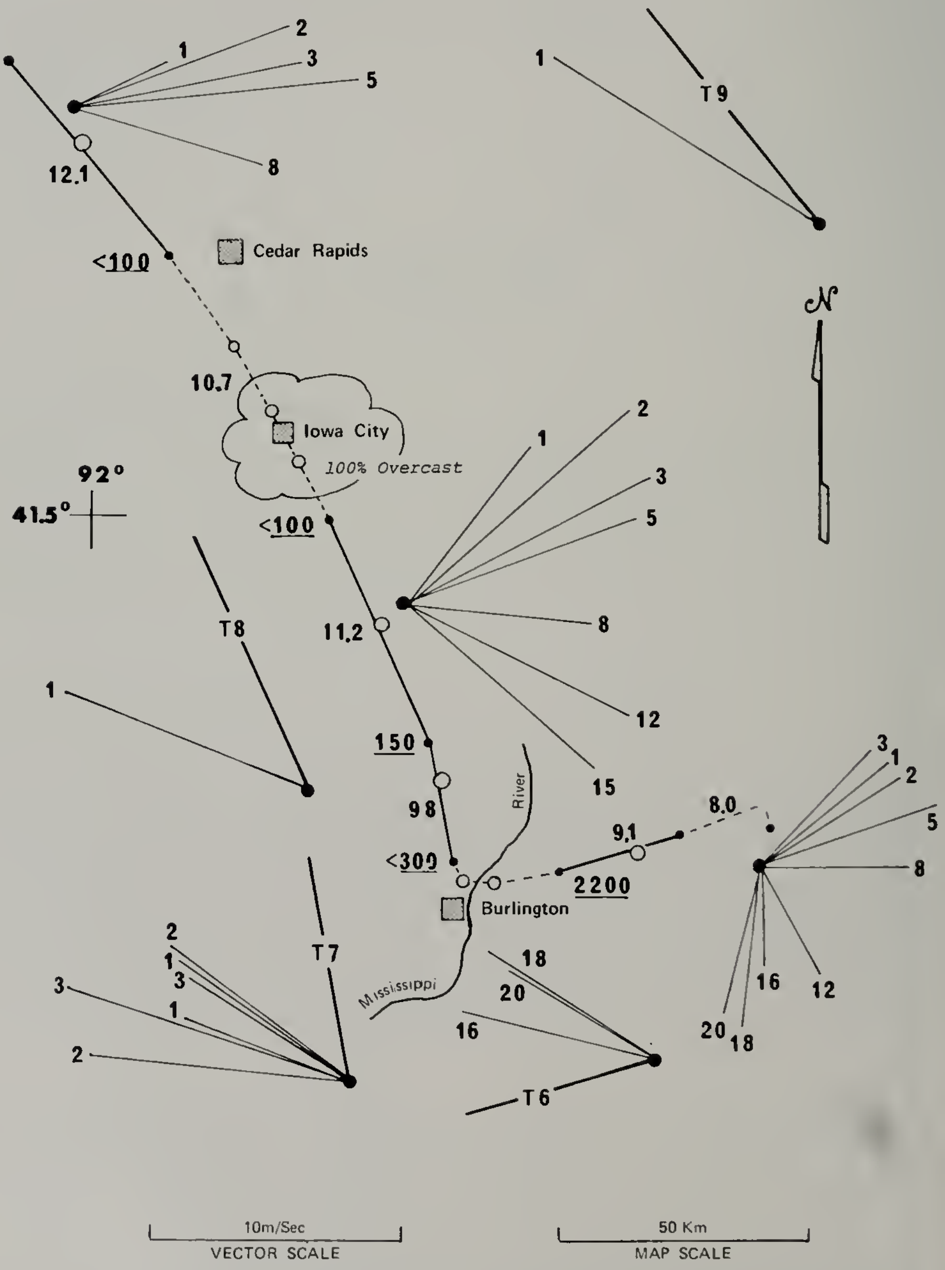
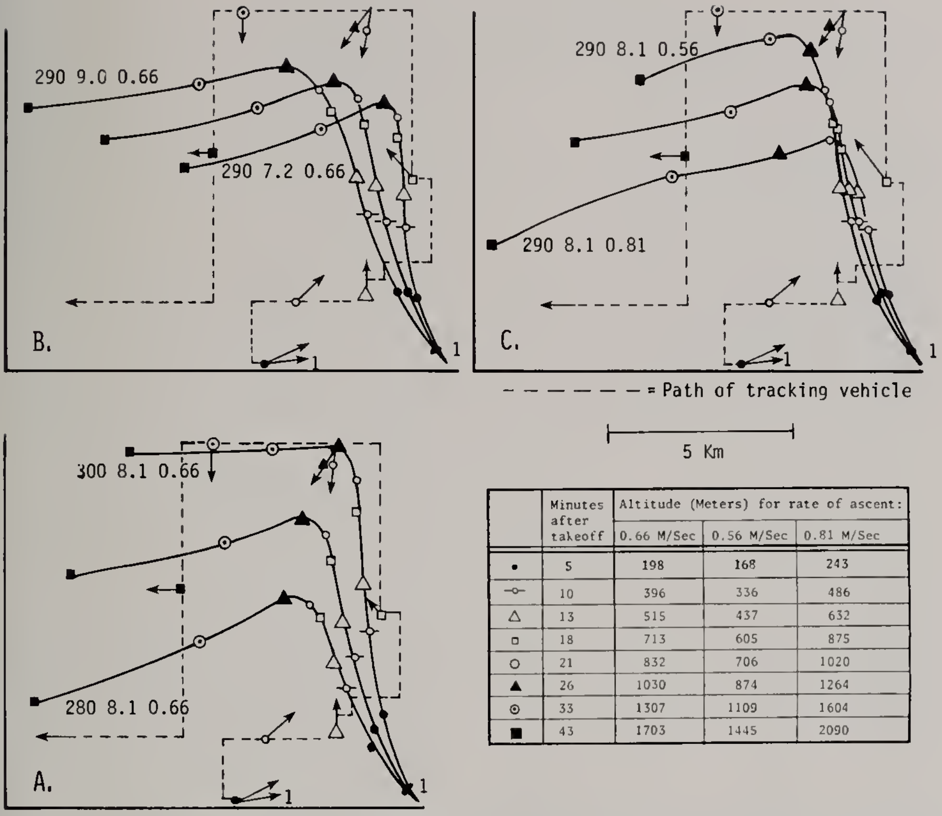


Fig. 5. – The approximate 24–25 May path of Swainson's 6905. Other information is shown as in Fig. 4, except that two sets of estimated headings are shown for T7, the upper set for winds measured at departure and the lower set for winds measured immediately to the north.



| | Minutes after takeoff | Altitude (Meters) for rate of ascent: | | |
|---|---|---|---|---|
| | | 0.66 M/Sec | 0.56 M/Sec | 0.81 M/Sec |
| • | 5 | 198 | 168 | 243 |
| -o- | 10 | 396 | 336 | 486 |
| △ | 13 | 515 | 437 | 632 |
| ▫ | 18 | 713 | 605 | 875 |
| ○ | 21 | 832 | 706 | 1020 |
| ▲ | 26 | 1030 | 874 | 1264 |
| ⊙ | 33 | 1307 | 1109 | 1604 |
| ■ | 43 | 1703 | 1445 | 2090 |

Fig. 6. – Computer simulated paths of a hypothetical bird ascending (at different rates, airspeeds, and headings), through winds aloft measured during the departure of Swainson's 6905 on 25 May (Fig. 5). Time-bearing data from the tracking vehicle and the route of the tracking vehicle are also shown. The central paths, in 6A, 6B, and 6C have the same 290° heading, 8.1 m/s airspeed, and 0.66 m/s ascent rate and thus are drawn identically. They nominally fit the observed time-bearing data. Alternate paths illustrate the effects of other values of these parameters. Arrows are bearings taken from the tracking vehicle. All times are in minutes after the bird took off. North is up. The take-off point and the position shown for minute 21 are the first two points plotted in the overall track of Fig. 5.

changed by 90° or more (Fig. 5). A simulation during this period would appear similar to Fig. 6 turned upside down, but the data during this period were sufficient only to indicate that the descent was more rapid than the prior ascent.

It is interesting to examine the options open to Swainson's 6905 on a heading of 290° at an airspeed of 8.1 m/s. Courses and ground speeds were calculated for the winds measured at altitudes reached by the bird (Table 2). These are the same as those used in the simulated plot of Fig. 6, but without the smoothing effect of interpolation of winds, which would cause Table 4 to be several pages long. Except for very near the surface, no altitude had winds that were favorable for flight on a course of 290°. At 950 m, lateral drift was near zero, but ground speed was reduced to about 2.2 m/s. The bird flew for about 60 km at altitudes above 950 m and incurred a 48° counterclockwise drift, but at a respectable ground speed of about 9 m/s. Later it chose near-surface flight with about a 50° clockwise drift, again at about 10 m/s ground speed. The bird appears to have preferred (or at least to have chosen) lateral drift to loss of ground speed.

Table 2. — Track directions and speeds calculated for real wind data (Table 4) and a bird with heading 290° and airspeed 8.1 m/s.

| Altitude (meters) | Track Direction (degrees) | Direction Relative to 290° | Track Speed (m/s) |
|---|---|---|---|
| Surface | 299 | +9 | 7.8 |
| 31 | 316 | +26 | 7.5 |
| 90 | 341 | +51 | 7.4 |
| 170 | 343 | +53 | 6.6 |
| 270 | 337 | +47 | 8.3 |
| 370 | 358 | +68 | 4.5 |
| 470 | 349 | +59 | 5.7 |
| 570 | 348 | +58 | 5.9 |
| 665 | 340 | +50 | 5.0 |
| 760 | 343 | +53 | 3.0 |
| 855 | 319 | +29 | 3.3 |
| 950 | 299 | +9 | 2.2 |
| 1,045 | 252 | −38 | 3.6 |
| 1,135 | 250 | −40 | 5.6 |
| 1,230 | 254 | −36 | 6.1 |
| 1,320 | 253 | −37 | 6.1 |
| 1,410 | 256 | −34 | 7.9 |
| 1,500 | 270 | −20 | 7.3 |
| 1,635 | 259 | −31 | 7.0 |
| 1,820 | 247 | −43 | 9.3 |
| 2,000 | 245 | −45 | 9.3 |

We observed only 12 cases of thrushes confronted by a choice between less lateral drift with lower ground speed and more lateral drift with higher ground speed. Although the results from a variety of analytical methods are similar, we present here an analysis of the component of track speed in the direction of the mean estimated (preferred) heading (progress speed) instead of the track speed. Progress speed is a measure of progress in the heading direction. Although the sample is small (Fig. 7), thrushes consistently "accepted" considerable lateral drift in avoiding progress speeds below about 6 m/s, choosing altitudes that resulted in reductions in lateral drift provided that progress speed was not reduced below about 10 m/s. An expected result of this selective behavior is the compression of the range of progress speeds (and ground speeds), a result reported in numerous radar studies. However, as will be shown, such a compression, for thrushes, is not significantly contributed to by altered airspeed.

We have indicated that Swainson's 6905 may have reduced drift by increasing airspeed during the latter part of its flight of 23 May (Fig. 4). An increase in airspeed may also have occurred on the flight of 24 May (Fig. 5). However, the increases (about 2 m/s or 20 percent) are of the same magnitude as the uncertainty in our estimated airspeeds. We examined airspeed data for the entire sample of Table 1. There appears to be no relationship (Fig. 8) between estimated airspeed and the deviation of track direction from the estimated heading (a measure of drift). Nor do we see a relationship between track speeds and airspeeds (Fig. 9), as has been indicated in several radar studies (see Larkin & Thompson 1980). Ground speeds for thrushes (Fig. 9) not listed in Table 1 tend to be high, because these thrushes flew mostly in tail winds (small or only slightly changing side winds) and, as has been mentioned, were for this reason among those not analyzed for drift. We believe the data show that if thrushes alter airspeed in response to lateral drift or to head or tail wind components, the response is limited to the order of 1 or 2 m/s.

## CHANGES DURING A FLIGHT — DRIFT REDUCTION

For the other thrushes tracked, with the possible exception of Swainson's 7012, insufficient data or winds that were less variable precluded modelling and detailed discussion like that presented for Swainson's 6905. However, it is useful to compare track directions near the beginnings and ends of flights with the preferred (mean estimated) heading (Table 3). In all but 1 of 16 flights, the difference between track direction and heading decreased during the night. The average difference was halved. The average rate at which the difference decreased was 5.5° per hour.

Several factors are not taken into account in this beginning-and-end an-

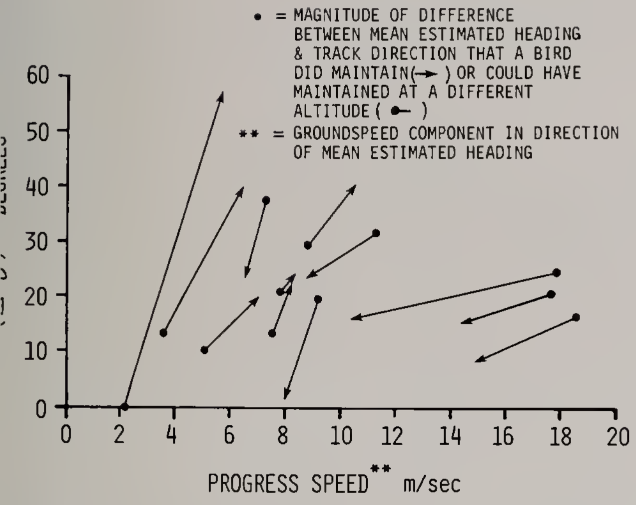


Fig. 7. – Twelve thrush choices between low progress speed with small deviation of course from a preferred heading and high progress speed with a larger deviation of course from a preferred heading. The dot is the option rejected, and the arrowhead is the option chosen. In each case the bird passed through the altitude where the wind provided the rejected option and levelled off at the altitude providing the chosen option.

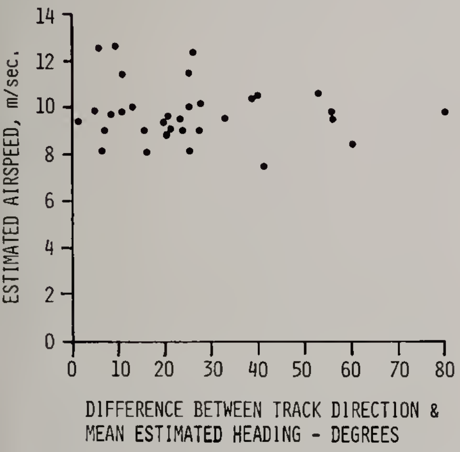


Fig. 8. – Estimated airspeed versus difference between track direction and mean estimated (preferred) heading. Data are from Table 1.

Table 3. — Track direction, relative to mean heading estimate, for an early and a late track segment in the same night's flight.

| Species, Year Number | Interval[a] (minutes) | Early Segment | | Later Segment | |
|---|---|---|---|---|---|
| | | Deg[b] | (TS)[c] | Deg[b] | (TS)[c] |
| He6910 | 136 | − 89 | (22) | − 47 | (24) |
| Sw6902 | 98 | + 23 | (14.5) | + 6 | (13.7) |
| Sw6905 | 370 | − 28 | (9.5) | + 7 | (8.0) |
| | 334 | − 41 | (8.0) | + 26 | (10.7) |
| Gc7003 | 183 | − 21 | (15) | + 7 | (16) |
| Sw7005 | 353 | + 19 | (14.4) | − 11 | (18.3) |
| Ve7008 | 113 | + 25 | (19.8) | + 18 | (10.6) |
| | 86 | − 21 | (23) | − 8[d] | (28)[d] |
| Sw7012 | 257 | − 53 | (14) | − 25 | (9.8) |
| He7015 | 161 | + 38 | (9.2) | + 1 | (10) |
| He7018 | 128 | − 28 | (9.0) | − 3 | (13.2) |
| Ve7103 | 63 | + 28 | (9.7) | + 42 | (13.8) |
| | 51 | + 51 | (16.3) | + 15 | (17.9) |
| Sw7118 | 360 | − 23 | (11.2) | + 14 | (10.6) |
| | 265 | − 21[d] | (19.3)[d] | + 16 | (15) |
| Gc7207 | 288 | − 40 | (11.3) | + 6 | (9.4) |
| *Mean* | *203* | *34.3*[e] | *14.1* | *15.8*[e] | *14.3* |

[a] Between the midpoints of the two compared track segments.

[b] Difference in degrees between track direction and mean estimated heading; plus indicates track direction clockwise from the mean estimated heading, minus counterclockwise.

[c] Track speed in meters per second.

[d] Data from track segment not given in Table 1.

[e] Mean of the absolute value of differences, sign ignored.

alysis. Birds were usually presented with different wind profiles near the beginnings and ends of flights. These differing wind profiles and the lack of accurate, continuous heading and speed data make it impossible to apportion the observed drift reduction among such possibilities as the winds becoming more favorable, the birds selecting altitudes with more favorable wind, or perhaps the birds slowly changing headings. The effect of changing wind is demonstrated by the first night's flight of Swainson's 6905 (Fig. 4). Unfortunately, we do not know exactly where the wind change occurred, but at an altitude of about 800 m the bird had achieved a track direction (seg-

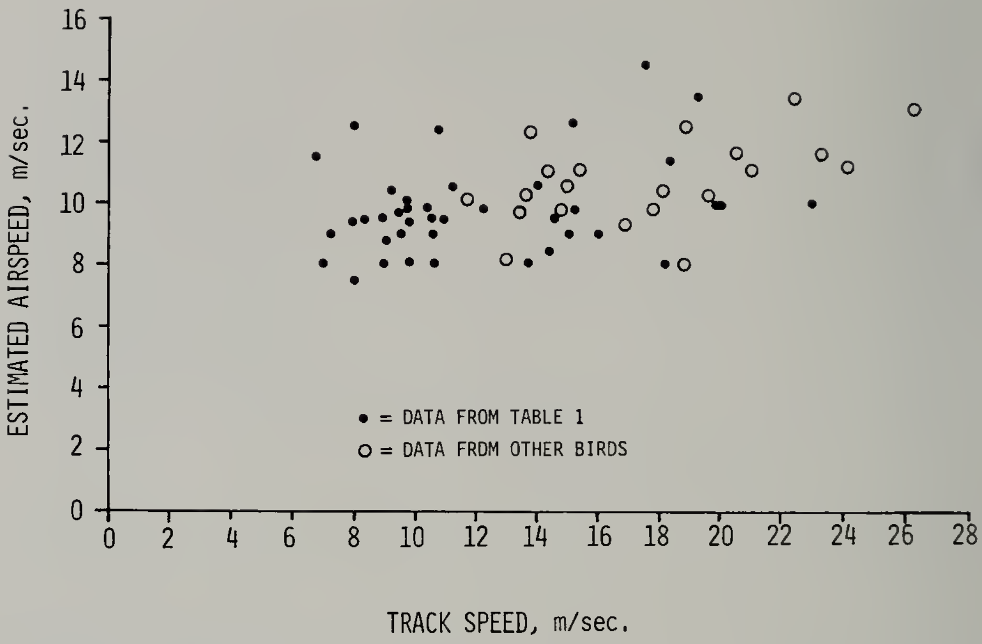


Fig. 9. – Estimated airspeed versus track speed.

ment T3) closed to its preferred heading. Then, presumably upon encountering changing wind, it reduced its altitude, and the track direction and speed changed markedly. A little later, at a still lower altitude, the difference between track direction and mean estimated heading was again reduced. It is tempting to assume that the process of finding an optimal altitude takes time and that, when different, less favorable, winds are encountered, a bird must repeat the process. If a bird repeats the process when less favorable winds are encountered, changing winds would tend to hinder a bird's efforts to find an altitude with winds optimal for its preferred heading and would tend to negate the compensatory effects of slowly altering its heading. Thus, the analysis derived from Table 2 probably understates thrushes' ability to reduce lateral drift. However, the data of Table 2 suggest that thrushes reduce drift over a period of time, that such reduction is accomplished without sacrifice of ground speed, and that the main method employed is altitude selection rather than change in heading or airspeed.

## ATYPICAL BEHAVIOR

Of the 36 thrushes tracked, veery 6901 was the only one to make a large heading change not attributable to storms. Data for it are included in Table 1 even though the wind varied little during the 3.5 hours the bird was tracked. The data plotted for this bird in Fig. 3 are given a special symbol. The veery did not maintain a constant course, a constant heading, or a constant heading relative to the wind direction. Instead, the bird turned clockwise (a heading change of at least 60°), as evidenced by both track directions and heading estimates. The turn could not have been an attempt to fly downwind, because the heading continued to change by 30° or more past the downwind direction. A delayed response to lateral wind drift is ruled out, because the indicated heading change was in the wrong direction. The sky was cloudless throughout the flight. We offer no explanation for the behavior of this veery.

Veeries 7008 and 7103 encountered thunderstorms and landed after changing heading away from head winds.

Table 4. — Theodolite measurements and computed winds aloft for the start of the 24 May flight of Swainson's thrush 6905.

| | Balloon | | Computed Wind | | |
|---|---|---|---|---|---|
| Minutes After Release | Elevation (meters) | Azimuth (degrees) | Elevation Angle (degrees) | Blowing Toward (degrees) | Speed (m/s) |
| 0.25 | 61 | 41.5 | 49.0 | 41.5 | 3.5 |
| 0.5 | 116 | 47.5 | 37.5 | 50.7 | 6.6 |
| 1.0 | 216 | 53.0 | 31.75 | 57.2 | 6.6 |
| 1.5 | 315 | 49.0 | 30.0 | 42.0 | 6.6 |
| 2.0 | 414 | 57.0 | 28.75 | 76.5 | 7.6 |
| 2.5 | 513 | 59.0 | 28.0 | 66.1 | 7.1 |
| 3.0 | 612 | 60.0 | 27.5 | 64.6 | 7.0 |
| 3.5 | 707 | 61.5 | 27.5 | 71.0 | 6.2 |
| 4.0 | 801 | 65.0 | 27.5 | 89.4 | 6.7 |
| 4.5 | 895 | 67.5 | 28.0 | 92.1 | 5.4 |
| 5.0 | 990 | 71.0 | 28.5 | 106.7 | 5.9 |
| 5.5 | 1,080 | 75.5 | 29.5 | 133.0 | 5.7 |
| 6.0 | 1,170 | 80.0 | 31.0 | 153.4 | 5.2 |
| 6.5 | 1,260 | 84.0 | 32.5 | 159.5 | 4.7 |
| 7.0 | 1,350 | 88.0 | 33.75 | 159.1 | 4.9 |
| 7.5 | 1,440 | 92.0 | 35.5 | 180.7 | 4.7 |
| 8.0 | 1,529 | 94.5 | 37.0 | 175.8 | 3.0 |
| 8.5 | 1,620 | 98.0 | 38.0 | 167.1 | 4.4 |
| 9.0 | 1,710 | 101.5 | 39.5 | 189.4 | 4.2 |
| 9.5 | 1,798 | 106.5 | 41.0 | 195.6 | 6.0 |
| 10.0 | 1,889 | 112.0 | 41.5 | 180.9 | 7.1 |
| 10.5 | 1,979 | 117.0 | 42.0 | 186.2 | 6.6 |
| 11.0 | 2,070 | 122.0 | 42.25 | 187.2 | 7.0 |

Data for the short track segments are listed in Table 1 but were not included in the TD-HE plot or in the means of the other track directions and heading estimates for these birds. Veery 7008 was approaching violent thunderstorms (frequent lightning was visible from the ground) between 2342 and 0038 CST but landed before encountering heavy rain. During this period the track direction and estimated heading shifted 45° and 35°, respectively. At the time the bird landed, the wind was blowing toward the south up to an altitude of at least 200 m, where the weather balloon disappeared into the cloud layer. Veery 7103 encountered a squall line with the surface wind blowing toward 170° at 7–11 m/s. We were north-northwest of the bird, awaiting its passage when these strong winds came up within a few minutes. Between 2148 and 2204 CST, we moved twice to the east and twice to the west to obtain bearings for triangulation and a heading estimate by the head-null method. Triangulation indicated that the bird was nearly stationary relative to the ground; heading estimates were 320° at 2152 and 2201 CST. While we drove back south to investigate, a sudden increase in signal strength indicated that the bird had changed heading. During the next 9 minutes the track direction was to the south-southwest until the bird landed in a dense woods just as the rain became a downpour.

## EFFECTS OF OVERCAST

Track directions and heading estimates for individual thrushes under clear, partly cloudy, and completely overcast skies provided tests for the effect of cloud cover.

Veeries 7008 and 7103, Swainson's 7118, and hermit 7015 (Table 1) collectively made eight transitions between clear and overcast skies. Similarly, Swainson's 6905 passed through a region with complete overcast (Fig. 5). Swainson's #5 and gray cheek #19 (Cochran et al. 1967) were observed under clear and overcast. In addition to these, three thrushes not included in Table 1 were observed under clear and overcast skies. These represent 15 transitions between clear and overcast sky, none of which was associated with a heading change. None of the 34 thrushes tracked during this study or the 21 thrushes studied by Cochran et al. (1967) was observed to alter heading during changes in cloud cover.

Migration was initiated under overcast skies by Swainson's 7012 and hermits 7015 and 7018 and by Swainson's #5, gray cheek #19 (Cochran et al. 1967), and one of the three thrushes observed under overcast in this study but not included in Table 1. We believe that the data show that thrushes are not affected by overcast skies present at the initiation of, or encountered during, migratory flight.

Griffin (1973) reported oriented flight of small birds in, above, and in between cloud layers. We were able to measure the altitude of flight and cloud ceiling for 12 thrushes tracked when there was a solid cloud layer. Of these 12, including the 10 discussed above, all flew below the clouds. A veery (Cochran 1972:Fig. 6) may be an exception. It was about 30 km east of the west shore of Lake Michigan at daybreak. The western lakeshore region was shrouded in heavy fog, but we could not tell how far the fog extended over the lake. The veery may have been flying over the fog, but certainly was unable to see the western shore even had it been high enough for line-of-sight viewing. The veery's track direction over Lake Michigan was within 10° of that observed during the preceding 560 km of flight, and it thus seems probable that this veery was well oriented in the absence of cues in the same sense that Griffin suggests for birds over clouds at more typical cloud altitudes.

## DISCUSSION

Wind drift is an important factor in the study of the orientation and navigation of migratory birds. In a practical sense, the responses of birds to wind determine the kinds of observations needed and how these should be interpreted. If individual birds maintained constant courses, a knowledge of their orientation behavior could be obtained directly, because track directions are measurable by most techniques. However, few of the many radar and visual studies give precise wind-altitude data, and none provides rigorous proof that individual birds maintain a constant course in variable winds. Analyses in all but a few of these studies have relied on assumptions about mean goals (intentions) of mixtures of unknown species (the radar swarm) arranged into sets flying in different winds. Even if species could be identified, assumptions about the goals of observed individuals could seldom be more precise than a quadrant. No matter how rigorous the mathematical and statistical treatment of models, radar observations, or visual observations, the validity of any conclusions can never exceed that of the underlying assumptions.

The constant-heading hypothesis finds partial support in several radar studies (Richardson 1976; Williams et al. 1977; Emlen & DeMong 1978). However, a majority of radar studies, at least 26 according to Alerstam (1976), indicate that the drift of the swarm is less than passive, i.e., there is partial compensation or no drift at all. If partial compensation is a reality for "average" behavior, we point out that it may result from mixes of individuals and species behaving differently, for example, some compensating completely; some partially; some flying downwind; and some, like the thrushes, flying a preferred heading. Bloch et al. (1981), in a study of European migrants, emphasize the mixture aspect but state that "Songbirds compensate drift due to a side wind at least partly by altering their heading; large individuals appear to be more successful in this than small individuals." Their separation of radar targets into five classes by echo signature and size analyses, although useful for some purposes, required assumptions about goal directions as in less sophisticated radar studies. However, the goal directions of migrants in Europe may be far more restricted than those of the western hemisphere thrushes, which as species breed and winter over a wide range of longitude.

In reference to radar studies in Illinois, Bellrose (1967:305) states that "all our evidence indicates that they correct within a few degrees for wind drift." It is difficult to reconcile our thrush data with this conclusion about the seasonal average behavior of the average trans-Illinois migrant. That thrushes select altitude for favorable winds would have shown up in radar data as pseudo drift (Nisbet & Drury 1967; Alerstam 1976), which increases apparent drift in the analysis of radar data and would add to rather than account for the discrepancy between our findings and Bellrose's findings. Graber et al. (1971) consider thrushes to be common migrants in Illinois, and both tower-kill data (Graber 1968; Seets & Bohlen 1977) and flight-call data (Graber & Cochran 1960) indicate that thrushes are among the most common migrants through Illinois in May and September. Therefore, thrushes should have been well represented in Bellrose's radar samples. Thrush species might be among the few that do not compensate totally, and it may be that their inclusion in Bellrose's averages was responsible for the "few degrees" of drift allowed for the average bird.

We have shown that thrushes reduce lateral drift as a night's flight progresses and that the reduction is accomplished primarily by the selection of an altitude with the least unfavorable wind and secondarily, if at all, by small, slowly implemented changes in heading and/or airspeed. Our data also suggest that when cross and opposing winds are the only options, keeping progress speed above about 6 m/s takes precedence over reduction of lateral drift, the latter having first priority only when progress speed exceeds 10 m/s. Thrushes landed when winds provided no options other than a progress speed of less than 2 m/s.

The ascent rates we measured for thrushes, between 0.3 and 0.7 m/s, are much less than the climbing capability of up to 4.4 m/s reported for passerines by Able (1977). Although high rates of ascent may not be as aerodynamically efficient as lower rates, the overall efficiency during a night's flight – in terms of distance covered per unit energy – would be improved for birds that quickly find the best winds available. If energy efficiency is improved by finding the best winds available as quickly as possible, and if thrushes are capable of faster ascents than those we observed, then their relatively slow ascent may indicate that the "measurement" process by which thrushes assess the effects of winds is an integrative one requiring a significant amount of time. This idea finds additional support in the considerable time (20–50 minutes) taken by thrushes 6809, 6810, and 7103 to respond (by landing) to extremely unfavorable winds and possibly in thrushes slowly altering their headings, as discussed below.

Some of our data suggest that if the optimal wind has a significant crosswind component, as it often does, thrushes respond by slowly altering their heading and perhaps airspeed as well. We reject the alternate interpretation, negative compensation, because there is no apparent benefit in a bird's increasing its lateral drift. Our data are not accurate or continuous enough for precise analysis, but they do rule out rates of change greater than a few degrees per hour. Corrections at such small rates could produce significant compensation for drift on long over-water flights in consistent wind but would be of limited benefit in the variable wind of the midwestern United States, particularly in spring, and for typical 6-hour overland thrush flights. We speculate that the ultimate degree of correction sought by slowly altering heading or airspeed may be set at limits imposed by progress speed, as suggested for corrections achieved by the selection of altitude for optimal wind.

Some of the thrushes we observed ascended, during the first hour or so of flight, through a variety of unfavorable winds and then descended to an altitude with winds more favorable than those encountered at higher altitudes. Some remained at a higher altitude with a wind no better than one encountered at a lower altitude. Still others ascended for a shorter period and levelled off at an altitude with an acceptable wind without testing higher altitudes for more acceptable winds. We note also that the ascent at the initiation of migratory flight is not repeated later in flight even if winds change significantly. Instead, after the initial ascent, altitude selection is restricted to descent or to small upward adjustments. These observations are consistent with a strategy of seeking a tolerable compromise through minimum effort rather than continuously seeking the most favorable wind available at all times. We believe that the energy expenditure required for major ascents, coupled with the low probability that major wind changes will occur during a night's flight, represent an energy-cost-to-wind-benefit ratio which favors the acceptance of a satisfactory compromise at hand as opposed to the continual seeking of a better compromise.

That lateral drift is reduced, by whatever means, and that low progress (or ground) speed results in the termination of flight, suggest that thrushes are aware of some aspects of their path vector, can assess the speed and direction of the wind relative to their heading, or some combination of both. Bruderer (1982:11) states that the ground is the "most simple and probable" reference by which the course is estimated. Bellrose (1967:306) speculated that birds may be capable of obtaining information about both speed and direction of wind, relative to their heading, from the "gust-form of air." If small scale accelerations of air (gusts) were used by thrushes to evaluate wind, it would seem that the evaluation could be done more quickly than our data indicate. For this reason and also because linear landscape features appear to be responsible for faster-than-usual course evaluation, as discussed below, we favor the explanation that thrushes use the ground as a reference for evaluating their situation much as a man might use objects on shore when paddling a canoe in a strong current.

Chicago (population about 7 million) and nearby Lake Michigan did not influence the flight headings of thrushes. Veery 7008 flew for 20 km over south and central Chicago before changing course and landing after encountering a thunderstorm. Two thrushes (gray cheek #7, Cochran et al. 1967; a veery, Cochran 1972: Fig. 6) flew essentially straight paths over Chicago and then out over Lake Michigan. Four others, not reported here because their flights were in unchanging winds, had straight paths over the Chicago metropolitan area. Unfortunately, none of these thrushes could be shown to be on courses markedly different from their preferred headings; therefore, we cannot dismiss the possibility that a bird flying in a strong crosswind as it encountered Chicago or Lake Michigan would use these major land features as references for course evaluation or correction, as is shown below for thrushes crossing major rivers.

Of nine thrushes that we have tracked across the Mississippi River, the course of only one, Swainson's 6905 (Fig. 5), changed in the vicinity of the river. The change in course is entirely attributable to the bird's descent to an altitude having a markedly different wind. The river and nearby Burlington, Iowa (population about 33,000), were prominent landscape features which may have enabled the bird to determine quickly that its precrossing course of about 254° was well off its approximately 295° preferred heading. Later in the same night, this thrush passed directly over Iowa City, Iowa (population about 35,000), and near Cedar Rapids, Iowa (population about 85,000), on a course that was 20°–30° to the right of its preferred heading without noticeably responding. However, during this time the bird was already flying so low that it could not have safely responded by descending. The paths of the other eight thrushes did not vary in the vicinity of the river, but their courses were within 20° of their preferred headings when they crossed it.

Of 17 thrushes that we have tracked crossing the Illinois River, Swainson's #5 (Cochran et al. 1967) was the only one whose course changed in the vicinity of the river. Its approximately 250° course prior to encountering the river was well off its 300° preferred heading. A descent was detected near the river. The course shift could have been entirely due to a change in winds at the lower altitude, but altitude data were too crude to preclude other possibilities.

The observations of Swainson's 6905 and #5 suggest that features of large rivers may provide better ground reference than the relatively featureless intervening landscape, despite a profusion of lighted small towns and cities. Perhaps cities are too bright or too new on an evolutionary time scale, or perhaps thrushes respond to linear landscape features only (e.g., rivers), as suggested by Bruderer (1982), but not to point features (e.g., cities), as proposed by Rabol (1974). Bingman et al. (1982:49) hypothesized "that migrants could utilize the Hudson River as a topographical reference by which to perceive wind drift from a preferred track and correct at least partially for these effects." However, they concluded that the birds altered their headings to achieve courses closely paralleling the river. That rivers are not followed by thrushes, even temporarily, is contrary to their conclusions and in agreement with James (1955).

Cochran et al. (1967:224) state, "Flights of less than an hour's duration sometimes occur during or before thunderstorm activity. These flights are downwind at low altitudes." Data gathered since 1966 do not support the downwind aspect of their conclusion. Instead, upon encountering a storm or squall line, thrushes adopted a heading that precluded upwind flight (and therefore was sometimes downwind) and always landed after changing heading, sometimes within minutes and sometimes after as long as an hour. We have not yet analyzed all the data bearing upon the question of thrush behavior in inclement weather and wish here only to remove any suggestion that downwind headings are specifically chosen.

However, regardless of wind direction, flights of radio-tagged wood thrushes [*Catharus mustelina* (Gmelin)] observed in Illinois during the last phase of spring migration to their nest sites were flying approximately downwind and at low altitude (Cochran unpublished data). At times and geographic localities where a low-altitude mix of radar or visual "targets" consisted of a considerable proportion of birds in the site-search phase, downwind distributions of track directions similar to those reported by Gauthreaux & Able (1970) might be observed.

Cloud cover had no effect on the headings of individual thrushes, whether encountered before or during flight. In this regard our thrush observations are consistent with the radar observations reported by Bellrose & Graber (1963). Able (1982) discussed the growing body of evidence for well-oriented flight under (and in) overcast and briefly reflected on what this may mean regarding orientation mechanisms. He concluded that "we appear no closer to understanding the mechanism by which this is accomplished than when Griffin (1973) discussed the problem nearly a decade ago." The data presented here add to the evidence for oriented migratory flight under overcast skies but do not reveal the mechanisms involved.

How can thrushes find their way between specific nesting and wintering areas separated by thousands of kilometers if they are largely at the mercy of the wind? We do not know, but winds do not make the feat as difficult as one might conclude at first glance. For example, we followed three thrushes for more than one night's flight and more than 400 km total distance each. The path of Swainson's 6905 was as serpentine as any we have observed, with track directions which varied more than 100°. Yet, after two nights of flight its azimuth from where we began observations at Champaign, Illinois, to near LaPorte City, Iowa, where we left it, was 308°, only 13° different from its preferred 295° heading. The overall path of Swainson's 7118 was 335°, only 5° different from its preferred heading of 340°; that of veery 7008 was 350°, not measurably different from its 352° preferred heading.

Long migrations made up of many shorter single night's flights are subject only to net drift according to the prevailing wind components of the various geographic areas traversed. The effects of weather systems will tend to cancel one another. Prevailing winds would necessarily shape any evolved system of navigation. The surprise in our data was that the net drift was remarkably small for such short path distances as 400–700 km in spite of the fact that the birds selected for presentation here drifted more than most of those that we observed.

Thrushes' constant-heading behavior, with wind drift mitigated by their seeking an altitude with, at worst, a not-too-unfavorable wind, represents a long-distance migratory stragety that, in view of the probability that net drift is negligible, is more conservative of energy than strategies involving complete or partial compensation for wind. We point out that nothing short of nearly perfect compensation for wind drift, especially for long migrations, can substantially reduce a distance-time penalty incurred by a bird in a homing process near the end of a migratory journey. Factors in addition to energy conservation are probably important in successful migratory strategies. For example, partial-compensation behavior may have an advantage over both complete-compensation and constant-heading behaviors on long overwater flights. Perhaps the advantages of partial-compensation behavior versus complete-compensation and constant-heading behaviors on long overwater flights could be examined on theoretical grounds, but we have not done so. We only speculate that the slow altering of heading, subject to restrictions on minimum acceptable progress speed, may have survival value for long overwater flights. Such behavior had such a small effect during short overland flights that we cannot be certain we observed it; therefore, if thrushes do alter headings and airspeeds slowly, the significance of such behavior would seem to lie elsewhere in their migratory journeys.

## CONCLUSIONS

1. Individual thrushes do not maintain a constant track direction (path over the ground) unless the wind they are flying in is also constant.

2. Individual thrushes maintain a constant heading during a night's flight and from night to night to an accuracy equal to or better than the ±3° precision of our best measurements, liable to the exceptions in 3 and 4 below.

3. Thrushes may change their heading in response to lateral wind, but if they do so, it is at a rate of change of less than about 3° per hour.

4. If thrushes alter their airspeeds to reduce lateral drift, they do so by less than about 2 m/s.

5. Thrushes' airspeeds (mean = 10.1 m/s, SD = 1.6) are independent of and less variable than their ground speeds (mean = 13.7 m/s, SD = 4.6).

6. Thrushes turn to avoid a headwind component (prior to landing) when they encounter thunderstorms.

7. Thrushes mitigate the effects of lateral winds by flying at altitudes where winds are not too unfavorable (see 8 and 9). After takeoff, thrushes ascend until they find suitable winds, but if these are not found below 2 or 3 km, they descend and either land or accept a compromise at a lower altitude, never below about 75 m. As winds change during a night's flight, thrushes adjust their altitude accordingly, usually by descending and rarely by ascending – but never to the altitude reached during the initial ascent.

8. If winds at all altitudes above about 75 m have unfavorable head and side components so that progress speed cannot be maintained above 2 or 3 m/s, thrushes land.

9. Thrushes choose winds for minimum lateral drift provided progress speed does not fall below about 6 m/s. When the choice is between lateral drift (up to about 60°) and progress speed (below about 6 m/s), thrushes accept the lateral drift.

10. The ascent rate of thrushes at the beginning of flight is usually in the range of 0.5–1.0 m/s. This rate is less than their climbing capability and may reflect the time needed for assessment of winds aloft.

11. Primarily because of (7) above and secondarily because of (3), (4), and the fact that wind speed typically declines during the night, thrushes' track directions become closer to their preferred headings toward the end of a night's flight.

12. Thrushes initiate and maintain constant (preferred) headings during migratory flights under, and during transitions between, clear, partly cloudy, and completely overcast skies, but they seldom, if ever, fly above the lowest unbroken cloud layer.

13. By implication from (7) above, thrushes either directly sense information about wind speed and direction (e.g., from anisotropies of small-scale turbulence), or they evaluate some aspect(s) of their progress over the ground, or both.

14. Prominent linear landscape features, such as large rivers, may enable thrushes to more effectively sense information about their progress over the ground.

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## APPENDIX

### DETERMINING LOCATIONS OF FLYING THRUSHES

Cochran et al. (1967:214) describe a method of determining the locations of flying thrushes by driving a tracking vehicle under them. This and other location methods require that the observers get close to a flying bird. From a knowledge of the approximate track speed and direction of a flying bird, a forward extrapolation of its flight path was plotted on a highway map. The places and times where the bird was likely to cross roads were noted. One of these road crossover places was selected by considering the average speed the vehicle could be expected to make in reaching the chosen place and the need to get there before the bird. Each new location of the bird was used to update the projected path and select the next crossover place. A general discussion of tactics and strategy are given in Cochran (1972:53–58). We point out here that tactics for keeping up with a bird are considerably different and more easily accomplished than those for making the repeated close passes necessary for gathering the best data.

Cochran et al. (1967: Fig. 4) employed a horizontally aimed eight-element yagi receiving antenna rotatable through 360° of azimuth. The antenna was equipped for reception of both horizontal and vertical polarization. This antenna provided horizontal directivity to a bird if the elevation angle to the bird was less than about 45°. For elevation angles less than 45° the signal was strongest (a peak) when the antenna was directed at the bird's azimuth, and it gradually weakened for azimuths on either side of the peak, reaching the minimum for azimuths in the vicinity of 90° from the peak. A second, much weaker peak occurred when the antenna was pointed directly away from the bird. As a bird entered a "cone" above the vehicle (elevation angles greater than about 45°), the relation between signal strength and antenna azimuth could not be interpreted, peaks and nulls appearing at numerous and varying azimuths. As a bird left the overhead "cone of uncertainty," the familiar relationship between antenna azimuth and signal strength returned. Positioning the vehicle for such an overhead passage (crossover) required selecting a place along the bird's projected path, as discussed above. At this place (ahead of the bird), the bearing to the bird was approximately 180° different from the bird's previously plotted track direction. In practice, the process of positioning the vehicle was iterative. The first location where the vehicle was stopped was only approximately correct. As the bird moved closer, bearing changes were noted, and the vehicle was moved forward or backward in an effort to place the vehicle directly in the oncoming bird's path. The process was sometimes frantic during the last moments, requiring rapid turning about or driving at high speeds in reverse. Sometimes the procedure failed, and the bird crossed the road well ahead of or behind the vehicle, a situation which, we will show, evolved into a method for determining both altitude and location.

Here we are interested in how the accuracy of the information gathered in this simple crossover procedure was estimated. In our study we made the receiving antenna moveable in elevation as well as azimuth (Cochran 1972: Fig. 4). With this alt-azimuth antenna mount, the cone of uncertainty was theoretically eliminated. In practice, because of the awkwardness of an alt-azimuth mount when directed in the near-overhead region, a cone of uncertainty remained for elevation angles above about 75°. By simple geometry it can be shown that (1) a bird must pass directly overhead for entry and exit bearings (into and out of the cone of uncertainty) to differ by 180°, and (2) for a bird's passage anywhere through the cone, the assumption that it passed directly overhead can err by no more than the altitude of the bird times the cosine of the elevation angle defining the edge of the cone. For example, for cones defined by 45° and 75° elevation angles and a bird at an altitude of 100 m, the bird must pass over a point on the road within ±70 and ±26 m, respectively, of the position of the vehicle. Except on the rare occasions when crossovers were detected while we were within sight of mapped landmarks, our errors in positioning the vehicle on a map were typically ±50 m due to map plotting and vehicle odometer precision and accuracy limitations. Therefore, for birds flying at 100 m or below, there was little point in worrying about cone entry and exit bearings. This situation was fortunate, because the rapidly changing angles to birds that flew past at low altitudes did not allow us to get more than crude bearings. At higher bird altitudes cone entry and exit bearings are more important. The errors discussed above for a bird at 100 m altitude become 700 and 260 m for a bird at 1,000 m altitude. However, when thrushes were flying high, there was time to take bearings carefully and to position the vehicle so that the bird passed near the axis of the cone. We conservatively estimate that, with the alt-azimuth mounted antenna used in our study, the crossover positions we plotted were never more than 200 m, and usually less than 100 m, from the actual crossing point.

Estimating the time of a bird's passage overhead required taking the mean of the times of its entry into and exit from the cone of uncertainty. A bird flying at a ground speed of 500 m/min (about 8.3 m/s) at an altitude of 1,000 m would pass through a cone defined by a 75° elevation angle in 62 seconds. In practice, these timings were never precise, especially for birds flying high, mainly because the transition into and out of the cone was never as distinct as presented here for purposes of explanation. It usually took five to ten transmitter pulses (about 5–10 seconds) to take a bearing and, failing in this, 10–20 additional seconds to determine that readings made no sense (the bird was in the cone). A similar delay occurred in determining that a bird had left the cone of uncertainty. Therefore, timings were usually late by 20 or 30 seconds. However, because track speeds were determined between successive crossovers, the systematic errors due to the delays tended to cancel one another. We believe our crossover timing error, as it affected track speed calculations, was rarely greater than 30 seconds, and from limitations imposed by the geometry of a pass, never as great as 1 minute.

The accuracy of the track directions and track speeds, as measured between successive crossovers, is estimated as follows. Assuming a worst-case 300-m error at right angles to a 20-km track segment, the error in computed track direction would be 0.85°. For a 20-km track segment flown at 8.3 m/s ground speed, a 30-second timing error would cause a 0.2-m/s error in computed track speed.

It was possible to measure altitude from two or more elevation and azimuth angles taken before and/or after a bird passed nearly overhead. Geometrically, one side and two angles define a triangle. In this case the length of the side was provided by track speed times the time interval between angle measurements. However, it was difficult to measure accurately the elevation angle to birds approaching head on or receding (tail view), because these aspects gave mixed polarization, which magnified errors caused by signal energy reflected from the ground. Errors in the elevation angle of only 10°–15° can cause errors of altitude measurement as great as 50 percent. Therefore, we used this triangle method only when circumstances precluded the use of the method described below.

We have mentioned that birds crossing roads ahead of or behind the vehicle provided a way of measuring altitude at the crossover point. The method is described and illustrated in Cochran (1972), but will be briefly recounted here. It requires that the track direction be known, preferably to within 10°, from prior data. The method is best described by example, starting with the tracking vehicle northwest of a bird holding a northerly course. The tracking vehicle is driven east as if a crossover place were to be determined, but is held back so that the bird will pass in front of the vehicle. While the bird passes in front of the vehicle, the transmitting antenna (and bird) present a side aspect, which gives pure horizontal polarization. Polarization is important, because the best elevation angles are taken when the polarization of the received energy is purely horizontal. When the azimuth to the bird is straight ahead (as the bird crosses the road), the time, odometer reading, and elevation angle to the bird are recorded. The vehicle continues moving east while azimuths are taken, and soon the azimuth is north (a second odometer reading is recorded at this time). Because the track direction is north, the vehicle is now at the place where the bird recently crossed the road (the crossover place is determined). The time of the crossover has already been recorded. The altitude of the bird as it crossed the road is the distance between the two odometer readings times the sine of the previously recorded elevation angle. The method is valid even if the path direction is not at right angles to the road, but the desired side aspect of the bird is, in practice, lost if path-road angles are less than about 45°. The trick is to be at a place on the road (when the bird crosses it) which gives an elevation angle in the useful range of 30°-70°.

Potential timing and positioning errors are not significantly different for this cross-ahead method from those for the crossover (overhead) method. The primary error in timing a crossing equals the product of the sine of the error in the first (presumed dead ahead) bearing, the distance from the place this bearing was taken to the road-crossing point, and the reciprocal of a bird's track (ground) speed. For a 5° bearing error, a 1-km distance, and an 8-m/s track speed, the timing error would be 10.9 seconds. The error in computing the place of crossing equals the error in distance measurement plus the product of the sine of the sum of the errors of the assumed track direction and second bearing taken, the track speed, and the time interval between first and second bearings. In the example above, an 80-m distance error, a combined track direction and second bearing error of 10° (these sum algebraically and may cancel), and a time interval of 41 seconds (vehicle speed of 55 mph), would cause a maximum crossover positioning error of 137 m (80 + 57). Altitude error equals the product of the difference between the tangents of the true and measured elevation angles and the sum of the distance and the distance error. For the above example, if the bird's actual crossover altitude was 1,000 m, if a 45° elevation angle was erroneously measured as 35°, and if there was an 80-m error in the measured distance the vehicle traveled between measurement points, then the calculated altitude would be 644 or 756 m for vehicle distance short or long, respectively.

The sensitivity of altitude computation to elevation angle error results in highly variable accuracy of altitude etimates (Table 1). We tested the accuracy of radio measurement of elevation angle against optical measurement to a transmitter attached to a kite and found that between 30° and 60° elevation, given time for numerous vertical sweeps of the antenna, errors were less than $\pm 3°$. In practice we seldom noted a consistency of elevation angle measurements which would suggest that their accuracy was within the few degrees indicated by the kite tests. One exception was Swainson's 7005, which had a continuous (instead of pulsed) transmitter that greatly facilitated measurement of elevation angles (and azimuth bearings as well).

The futility of using U.S. Weather Bureau (USWB) winds-aloft data is illustrated by the impossibility of analyzing the flight of Veery 6705 (Fig. 2), which was tracked before we obtained winds-aloft measuring equipment. This veery flew at different altitudes in winds which varied greatly with altitude, time, and geographic location. The veery descended as it passed through a slowly moving warm front with large shifts of the lower-strata winds north of the front. A case for a variety of behaviors could be made by choosing particular winds-aloft data from those available from the USWB for different times and places. Only constant-course behavior (complete compensation) can be excluded. We invite the reader to apply compass and rule to data of Fig. 2, which is scaled accurately enough for this purpose. Sometimes birds did fly close to USWB stations when winds aloft were being measured, e.g., thrushes #5 and #19 (Cochran et al. 1967) discussed in the text. The probability of this occurring was small in the 1960's and is lower now, because times when and places where the USWB measures winds aloft have greatly decreased. For example, we did not measure winds aloft when Swainson's 6905 passed south of Peoria, Illinois, around midnight (Fig. 4), because we counted on obtaining the 2315 USWB measurements. When we went to the USWB for their data, we were told that they no longer measured winds at 2315 hours, a severe disappointment, as this wind information would have allowed us to analyze the middle portion of the flight. Even when USWB winds-aloft measurements were available for the place and time of a bird's passage, they were of limited use when wind shear was high, because they are computed for increments of about 500 m (above about 800 m). Some USWB wind data we examined showed a 180° shift between two adjacent 500-m levels! We do not imply that USWB personnel were ever less than helpful and cooperative; in fact we found that they would, for cost, given an hour or two of advance notice by telephone, measure winds aloft at times we specified. On several occasions, when we saw that a bird was headed toward one of their stations, we took advantage of this service. The widely distributed network of USWB stations with its capability for winds-aloft measurement represents a useful and accessible resource.

We calculated winds aloft from theodolite measurements of elevation and azimuth angles to ascending helium-filled balloons. We took readings at 15, 30, 45, and 60 seconds, and at 30-second intervals thereafter. These intervals provided wind data for altitudes of 30, 100, 150, and 195 m and at about 100-m intervals at higher altitudes. The theodolite was calibrated by sighting the north star or by a corrected magnetic compass sighting when the sky was cloudy. The horizon was established by a bubble level. A light was attached to the balloon for night readings, but this was unnecessary for measurements started 30 minutes after sunset or before sunrise, near the usual beginning and ending times of thrush flights. We tested how accurately balloons conformed to the assumed ascent rate by measurements from two theodolites. For six test ascents actual altitude did not deviate from the standard rates (for a 30-g balloon) by more than 2 percent. Measurements taken at the beginning of the second night of flight of Swainson's 6905 (Fig. 5) are listed in Table 4. Note that we missed the 45-second reading in this set. Missing one of the first few readings was common because of the difficulty in keeping the theodolite pointed at the nearby balloon as the balloon rapidly changed azimuth and elevation. We measured winds aloft before and after flights and as often as circumstances permitted during a flight.

Calculated heading estimates (those with associated track speeds in Table 1) were obtained by using standard trigonometric equations (on a computer) instead of the equally valid but more time consuming graphical method illustrated in Fig. 4 and 5. The accuracy of track and wind vectors we measured was usually good enough for the calculation of approximate path vectors (near where winds were measured) to an accuracy of ±1° or 2° and 0.5–1.0

m/s. Unfortunately, altitude measurements were usually too inaccurate to permit an unambiguous choice of winds to use for the calculations. Therefore, lack of accurate altitude data and/or lack of wind data at particular places precluded the use of most of the tracking data gathered during the study. Calculated heading estimates (±3°:Table 1) resulted under ideal conditions when wind did not change significantly over the range of altitude estimates. We applied a 3° uncertainty to all heading estimates as a conservative lower limit to the error range for calculations from measurements taken under these ideal circumstances. Appropriate (higher) error ranges were applied when added uncertainty resulted from less than ideal track or wind vector data or when wind varied significantly over the range of altitudes estimated for a bird. Headings were excluded from the data set when the estimated errors exceeded about ±10°.

## TAKING HEADINGS BY METHODS NOT REQUIRING WIND AND ALTITUDE DATA

To understand these methods, it is useful to visualize the aspect, i.e., the projection, of a trailing wire antenna (on a bird) on an observer's plane of vision, as viewed from various places. For purposes of discussion, we consider the antenna wire to be straight and to pass directly over the bird's tail parallel to the earth. Viewed from directly ahead of or behind a bird (at the bird's altitude) the wire is invisible (has a point aspect). Viewed from ahead or behind, but from the ground, the wire appears as a vertical (to earth) line which subtends a smaller viewing angle than if the wire were turned broadside to the viewer (wholly in his plane of vision). This apparent shortening of the wire is called "foreshortening." The maximum amount of energy which can be received from a wire antenna is proportional to the ratio of the foreshortened aspect to the broadside aspect (the wire in the observer's plane of vision), or simply, to the sine of the viewing angle (Va), which is 0° from head on and 90° for a broadside view. We say "maximum amount of energy which can be received" because, for an antenna pointed at a bird, the signal actually received depends on the relative orientation between the receiving antenna elements and the aspect presented by the transmitter antenna wire. In the example above (a view from the ground ahead of the bird) the wire antenna on the bird appears foreshortened and vertical. If a receiving antenna with elements vertical to the ground is pointed at the vertically appearing transmitter wire antenna, it will receive all the energy available. Conversely, if the receiving antenna elements are horizontal, none of the available energy will be received. In contrast, viewed from the side there is no foreshortening (sine 90° = 1); so the maximum amount of energy will be received, but only if the receiving antenna is held with elements horizontal to match the horizontal aspect of the wire. Matching polarization maximizes signal and crossing polarization nulls the signal. More concisely, the received signal strength is proportional to the cosine of the angle between the relative aspects of the receiving antenna elements and the transmitting antenna wire, which we call the crossing angle (Ca). Thus, from any point the received signal is proportional to the product of sine(Va) and cosine(Ca). Therefore, received signal strength is maximum when Va=90 and Ca=0, and zero when Va=0 or Ca=90. We stress the logical use of *and* and *or* in the preceding statement. It is unfortunate for discussion's sake that Va and Ca cannot in all cases be conveniently expressed in an orthogonal system relative to the earth's surface. However, the following statements are true for head-on, side, and underneath positions of an observer, the special cases where these angles bear an orthogonal relationship to the earth's surface.

1. The strongest signals are received when an observer is to the side (Va=90) using horizontal (to earth) polarization (forcing Ca=0).
2. A weaker signal is available from directly ahead of (or behind) a bird (Va = elevation angle to bird) and is maximized by using vertical polarization (forcing Ca=0).
3. A zero signal is received for horizontal (to earth) polarization (forcing Ca=0) only when directly ahead of (or behind) a bird.
4. A zero signal is received for a bird overhead (or below) by forcing Ca=90.

## THE HEAD-NULL METHOD

This method required measurement of the azimuth to the bird while conditions (2) and (3) above apply. Although it is theoretically possible to verify geometrically a directly ahead (or behind) position by noting a finite signal with vertical polarization (2 above) and a zero signal with horizontal polarization (3 above), it is impossible to confirm a zero signal, because no matter how sensitive a receiver is, a signal always disappears into the receiver's background noise before the signal becomes zero. In practice, the head-null method required driving the tracking vehicle across the dead-ahead-of-the-bird position and noting the disappearance and reappearance of the horizontally polarized signal and the corresponding azimuths to the bird (obtained by using the vertically polarized antenna). Dead ahead (of the bird) refers to the bird's heading and not to the projection of its course (probable path). When the tracking vehicle is a small distance (relative to the distance to the bird) on either side of dead ahead of the bird, the strength of signals from both horizontally and vertically polarized receiving antennas is very sensitive to the elevation angle and the angle subtended at the bird by the tracking vehicle and the dead-ahead azimuth. Both of these angles are small and change rapidly as the distance from the oncomng bird decreases. The net result of the angular asymmetry thereby introduced between points equidistant on each side of the dead-ahead-of-the-bird position, compounded by the difference in distance to the oncoming bird at these two points, is that the azimuth for Ca=0 (corresponding to the dead-ahead vehicle position and from which the bird's heading is determined) is not the mean of the azimuths of the disappearance and reappearance of the horizontally polarized signal. The asymmetry and distance problems are compounded on a road which angles toward the bird and are mitigated on a road which angles away from the bird, the degree of compounding or mitigation depending on the angles and distances involved. For these reasons and because it is practically impossible to correct quantitatively for them, this method is best executed at a high vehicle speed which approximately "freezes" the overall geometry while the azimuths of disappearance and reappearance are being measured. This "freezing" is more closely approximated for a bird several kilometers distant, because the angles and distance to the bird are limited to smaller percentage changes during the time required for vehicle movement. Unfortunately, the signals from a more distant bird are weaker due to distance and small Va and elevation angle, which move the places for signal disappearance and reappearance farther apart and require the vehicle to cover a greater distance during the measurements. Additionally, it is harder to measure bearings accurately when travelling at high speed, and roads which were not at right angles to a bird's heading, as was the usual case, further complicated execution and interpretation. Therefore, the high precision typical of null measurements could not be realized in practice with the head-null method. The error range for the head-null estimates used in this paper (Table 1) was determined from the disappearance and reappearance azimuths, which were definite bounds to the actual heading. We never purposely executed this method by crossing behind a bird, because falling behind was too often associated with permanently losing contact with a bird. An optimal tactic was to cross in front for a head-null estimate of heading and to turn around and obtain a crossover location and an altitude estimate by the means previously discussed.

## THE CROSS-POLARIZATION METHOD

The cross-polarization method of obtaining a heading estimate is conceptually simple, a matter of getting under the bird and as in (4) above, rotating the receiving antenna about a vertical axis until a null indicated Ca was equal to 90°. This method was a natural companion to the crossover positioning method described previously. When the bird was in the cone of uncertainty, it was also in position for rotating the vertically pointed yagi antenna to the null position (Ca=90°) and reading this position directly on the azimuth compass rose. In practice this maneuver was difficult, especially for birds at lower altitudes, because birds were not in the cone of uncertainty long enough to allow us to take good measurements. Actually, the cone of uncertainty represented a zone of confusion for the antenna operator, and it was not until late in the study that we became skillful in executing the cross-polarization method. We consider ±4° to be a sufficiently conservative base error range for these measurements, which were precise to 1° or 2° relative to the azimuth of the vehicle. The major source of error was in the vehicle's azimuth. The three cross-polarization heading estimates for Swainson's 7118 were obtained from an aircraft circling high above the bird. In general, an aircraft would be an excellent platform from which to use the cross-polarization method if a belly-mounted dipole antenna could be rotated from inside the aircraft. In the case of Swainson's 7118 we used a hastily rented aircraft and pilot and were forced to use an antenna clamped to the footstep. The aircraft had to be circled without banking it (using rudder only) alternately clockwise and counterclockwise, because the antenna was not mounted symmetrically on the airframe. The mean of 10–12 readings, (half taken during clockwise circling), which ranged over 10° in azimuth, was used for each of the estimated headings. Frequent gyroscope calibration was required. Only three heading estimates were obtained because of time taken in navigating, fueling, locating the bird, and determining its altitude by the crude proximity method described in Cochran (1972). The last heading estimate was obtained as the bird descended through a large wind shear, and the associated track segment is without a track speed (Table 1) because the end point of the segment is where we located the bird on the ground without having detected the exact landing time.

## IN SUMMARY

The procedures and methods are described above as set-piece operation, the making of a specific measurement at a specific time or when a certain situation pertained. In reality, bird tracking was more chaotic and required the gathering and recording of a large amount of potentially redundant data without knowing beforehand which would be good enough and which would be acquired at the right places and times to be useful for analysis. For example, we mentioned taking an elevation angle when the azimuth to a bird indicated that it was crossing a road ahead of the vehicle. In practice, azimuths and elevations were continually taken and recorded as the vehicle sped toward the bird. As likely as not, no good set of measurements was available for the dead-ahead position, but was available when the bird was at some small (less than 20°) angle to the right or left of dead ahead. The geometry of all of the methods described is somewhat tolerant of deviations from the ideal situation as long as the deviations are taken into account. More often than not, attempts to execute the various procedures failed. We were fortunate that the data from the relatively small percentage of successful executions were sufficient to address the question of wind drift in thrushes.

The equipment used in this decade-old study was primitive by the standards of 1983, but the geometries of the methods remain fixed. Today, greater quantities of more accurate data could be obtained by the use of microcomputer control of several vehicle-mounted antenna systems, each specialized for gathering data appropriate to the geometry of a particular method.

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# Afternoon Session Summary

James R. Karr

A 50th anniversary symposium or even the centennial meeting only 25 years ago would no doubt have been very different from that held in 1983 to commemorate the 125th anniversary of the Illinois Natural History Survey. Noteworthy differences might include the conceptual context of the scientific questions addressed and, especially, the increased technological dependency of late 20th-century biological science. But commonalities would also be obvious, the most important of which would be the firm foundation in natural history and the use of that knowledge in the interpretation of pattern and process in nature.

Each paper in the afternoon session draws on its own unique combination of these and other factors. Goldman takes his title from the classic paper of Stephen A. Forbes and forges an impressive array of observations and insightful interpretations to account for changes in Lake Tahoe. He demonstrates the importance of long-term research, of the integration of observations of apparently unrelated phenomena, indeed of the perseverance required to accumulate sufficient information to demonstrate pattern in nature and the process that generates and, in this case, degrades natural resources of considerable value.

Goldman's work at Lake Tahoe, like research that led to improvement of the Thames River (Gameson & Wheeler 1977) and Lake Washington (Edmondson 1977), demonstrates that the causes of environmental degradation can be identified. The work at Tahoe parallels studies of the Illinois River conducted by staff of the Illinois Natural History Survey (Mills et al. 1966; Starrett 1972; Bellrose et al. 1983). The challenge for the Natural History Survey in the future is to do for Illinois streams what Goldman has done for Lake Tahoe. But the lesson of Lake Tahoe is more than "the lake is damaged and may even face ecological destruction" – the land itself may be destroyed as well through erosion and other degradation. In Illinois we must take action to protect rivers *and* the land they drain. Without them even the most innovative technological society faces overwhelming environmental crises.

The second paper of the afternoon session is concerned with very different geographic and biological scales. The concern of Philipp, Kaminski, and Whitt about the genetic integrity of largemouth bass populations develops from a careful integration of natural history, population genetics, and evolution. The application of new technologies to identify genetic traits allows a more sophisticated view of the responsibility of fishery managers and, indeed, of resource managers in a broader context. The folly of mixing gene pools of northern and southern largemouth bass is demonstrated through documentation of the negative effects of careless stocking programs on regionally adapted populations. We see modern technology, allowing sophisticated analysis of pattern, combined with good old-fashioned natural history to yield the potential for more informed management of natural resources. More conventional forms of management techniques, such as habitat manipulation, harvest regulation, propagation, and stocking, must be combined with genetic management.

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Page reviews reproductive behavior and its evolution in about 150 species of percid fishes. Spawning behavior provides the focus for an analysis of an array of life-history attributes that vary in concert with reproductive behavior. The accumulation and integration of detailed information on the biology of many species provide a foundation for the synthesis of theoretical insights and help to define management options and strategies.

With Cochran and Kjos we emerge from the water to explore the biology of bird migration. Specifically, they deal with the problems posed by wind and overcast skies for thrushes on the long voyage between breeding and wintering grounds. I can attest to the precision of these navigational skills because, like others, I have had migrant warblers and thrushes return to the same wintering territory in Panama after annual trips to breed in North America.

Cochran and Kjos document the ability of thrushes to compensate for wind and cloud cover during migration. With an insightful combination of technical sophistication and natural-history wisdom, avian migration is not made simple, but it at least becomes more comprehensible. Cochran and Kjos show that thrushes have preferred flight directions and speeds for accomplishing their navigational feats. They seek winds at a variety of heights that provide for these preferences. When winds are such that flight speeds are reduced to less than 2 m/s, the birds simply land and wait for better conditions.

Throughout this set of papers, natural-history information accumulated laboriously from tedious observations over extended periods combines with sophisticated applications of modern technology and biological theory to yield knowledge of factors that will, when taken collectively, provide the opportunity for better management of natural resources as well as greater understanding of our natural world.

As I listened to these presentations, several general thoughts came to mind. These thoughts involve inherent difficulties in the integration of knowledge from various biological disciplines and the incorporation of that knowledge in a broader societal context.

1. The study of organisms and the interpretation of natural-history data are key responsibilities of the Natural History Survey. The job has been well done in the past but will become more difficult in the future because biologists face the same problem that herbivores face in dealing with plant chemistry while feeding and in avoiding predators. In the evolutionary battle between food and feeder, each is constantly trying to get one step ahead of the other. In a very real sense human society is on the same treadmill in the use of pesticides (evolution of pest resistance) and technology (the inability of biological systems to change rapidly enough to survive the growth of that technology). I am confident that, unless we destroy the biological systems of earth, including ourselves, no long-term panacea will be forthcoming because of the evolutionary process. In the end, *Homo sapiens* as we know the species may simply become extinct through evolutionary processes much as *H. erectus* was replaced.

This continuing evolutionary process is both good and bad. Good because we can continue to enjoy the vitality, excitement, and challenge of biological research; bad because we will always be racing to keep up with insults to the integrity of our planet's thin biological mantle while we try to extract goods and services from that mantle.

2. The biologist's perspective must always be both microscopic and macroscopic. Short-term or local solutions should not be used without careful evaluation of their probable long-term and regional (even national and international) implications. Perhaps the most difficult task facing biologists will be the integration of information obtained over a hierarchy of spatial and

temporal scales. We must simultaneously take a close look at detail while standing back to view systems as integrated wholes.

3. Interactions between basic and applied biologists have often been less than satisfactory. Many theoreticians, often with limited field experience, have looked down upon managers, perhaps because of a disdain for mission-oriented research. Conversely, resource managers have been reluctant to evaluate the merit of recent theoretical developments, perhaps because they are too "esoteric." That the two can effectively merge, indeed depend on each other, is demonstrated by the papers presented here and by the research going on at INHS. The complexity of important resource issues requires the effective merger of the two camps and cooperation to their mutual benefit.

4. As I have noted several times, a substructure of systematic and natural-history information (of inherent value on their own, as are music and art) is essential as a backdrop for virtually all natural-resource decisions. Theoretical considerations alone are inadequate for informed resource management.

5. Finally, biologists must recognize their insights and integrate them into the social, political, and economic contexts in which societal decisions are made. Biologists can no longer advocate policies that ignore any of these realities. Similarly, economists, politicians, and others cannot ignore long-term trends in the degradation of life support systems as if they were not relevant to current and future conditions for human society. If biologists do not participate as equal partners, biology will be ignored, or perhaps worse, we will continue to base decisions on the input of those not familiar with the facts of biology.

In summary, challenges to biologists for the future are immense. Looking back on the last 25 years, I see growth and intellectual vitality. I expect the future to be even more exciting and look forward to learning more about the growth at the 150th anniversary celebration of the Illinois Natural History Survey.

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