Phylogenetic Constraints, Adaptive Syndromes, and Emergent Properties: From Individuals to Population Dynamics

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Abstract. The hypothesis is developed that there are causal linkages in evolved insect herbivore life histories and behaviors from phylogenetic constraints to adaptive syndromes to the emergent properties involving ecological interactions and population dynamics. Thus the argument is developed that the evolutionary biology of a species predetermines its current ecology. PHYLOGENETIC CONSTRAINTS refer to old characters in the phylogeny of a species and a group of species which set limits on the range of life history patterns and behaviors that can evolve. For example, a sawfly is commonly limited to oviposition in soft plant tissue, while plants are growing rapidly. ADAPTIVE SYNDROMES are evolutionary responses to the phylogenetic constraints that minimize the limitations and maximize larval performance. Such syndromes commonly involve details of female ovipositional behavior and how individuals make choices for oviposition sites relative to plant quality variation which maximize larval survival. Syndromes also involve larval adaptations to the kinds of choices females make in oviposition. The evolutionary biology involved with phylogenetic constraints and adaptive syndromes commonly predetermines the ecological interactions of a species and its population dynamics. Therefore, these ecological interactions are called EMERGENT PROPERTIES because they are natural consequences of evolved morphology, behavior, and physiology. They commonly strongly influence the three-trophic-level interactions among host plants, insect herbivores, and carnivores, and the relative forces of bottom-up and top-down influences in food webs. The arguments are supported using such examples as galling sawflies and other gallers, shoot-boring moths and beetles, budworms, and forest Macrolepidoptera. The contrasts between outbreak or eruptive species and uncommon and rare species with latent population dynamics are emphasized.

Key words: eruptive populations, female preference, larval performance, latent populations, life history evolution, population dynamics.

Introduction

G. Evelyn Hutchinson (1965) called his book "The Ecological Theater and the Evolutionary Play." The theme developed was that ecology sets the scene for evolutionary processes. However, the evolutionary changes he discussed were *microevolutionary* in scope such as character displacement. Hutchinson's view was appropriate for the small details of adaptation to environment including abiotic and biotic factors, and community organization.

However, for understanding in a comparative way broad patterns in nature it is more likely that the reverse of Hutchinson's view is most valuable. That is, the evolutionary background formed over a very long phylogenetic history provides strong influences on the current ecology of species. So if we study MACROECOLOGY, or large-scale

patterns in nature, then we may learn new insights by recognizing the MACROEVOLUTIONARY background of the species we wish to study. Thus, the subtitle of this paper could be "The Macroevolutionary Theater and Macroecological Play."

This viewpoint is important in my opinion in the study of three-trophic-level interactions which define the population dynamics of insect herbivores. The three trophic levels involve plants, herbivores, and carnivores, and major differences in evolved life histories and consequent individual behavior, influence profoundly the way in which plants and herbivores interact, and herbivores and carnivores interact in an ecological context. Thus for broad-scale comparison of patterns in these relationships I argue that the phylogenetic history of species should be the *starting point* for an understanding of insect herbivore popula-

tion dynamics.

By understanding the evolutionary background of species I think we can understand their *potential* ecological relationships which may be observed today. However, on top of the evolutionary background, ecological relationships may be superimposed. Therefore, species with the same evolutionary background may illustrate different population dynamics because of differences in ecology. Disentangling the evolutionary potential from ecological reality is a challenge I will address towards the end of this paper. In the mean time, I will concentrate on *macroevolutionary* differences between groups of species and how these influence the potential for population dynamics in these groups of species.

The phylogenetic constraints hypothesis

The key macroevolutionary traits of a species relevant to its population dynamics can be called PHYLOGENETIC CONSTRAINTS. These are ancient characters in the phylogeny of a group of species which set limits on the range of life history patterns and behaviors that can evolve (Price et al. 1990). For example a sawfly, with its saw-like ovipositor, is commonly limited to oviposition in soft plant tissue, so that multiple use does not wear out the saw. This means that life histories must result in the phenological overlap of young, rapidly growing plants and plant parts and the occurrence of sawfly adults. This in turn limits the range of life histories that can evolve. So the saw of a sawfly becomes an ancient phylogenetic constraint on the current evolution and ecology of the species.

Such limitations or phylogenetic constraints are reduced by a set of adaptations that I call the ADAPTIVE SYNDROME. Adaptive syndromes are evolutionary responses to the phylogenetic constraints which minimize the limitations and maximize larval performance (Price et al. 1990). For example, although a sawfly is constrained to oviposit in freshly growing young shoots, there exists the adaptive opportunity for evaluating food quality for her progeny, and for selecting plant parts most suitable for larval growth and survival.

In this way the macroevolutionary background of a species, identified as phylogenetic constraints and adaptive syndromes, sets the stage for macroecological patterns in population dynamics. The evolutionary theater predetermines the ecological interactions of a species and its population dynamics. Therefore, I call these ecological interactions EMERGENT PROPERTIES because they are natural consequences of evolved morphology, behavior, physiology, and life history. For example, a sawfly species that evolves with the ability to select high-quality resources for progeny may well become limited at the population level by these resources. If resource supply is

stable over time then stable population dynamics of the herbivore is likely to be dictated by this bottom-up influence in the trophic system.

This interplay of phylogenetic constraints, adaptive syndromes, and emergent properties helps to identify the relative forces moving up and down trophic systems in three-trophic-level interactions. Evaluation of bottom-up effects from plants, and top-down effects from carnivores on insect herbivore population dynamics is possible because evolutionary and ecological factors are integrated in this approach (cf. Hunter and Price 1992).

I have chosen to call this the Phylogenetic Constraints Hypothesis because it focuses attention on what is the key to understanding broad patterns in nature, in my opinion. The key is the differences in behavior and life history on a macroevolutionary scale which have had repercussions down the lineages to what we observe currently in the ecology of related species, including population dynamics.

The evolution of life histories: applying the hypothesis

The hypothesis can be applied to groups of species with very different life histories. I will use two extremely different types of life history, which probably illustrate the ends of a continuum to be found in nature. I will argue that these evolved differences in life history have inevitable consequences for the potential and actual differences in population dynamics of the species concerned. The two types can be found together in almost any north temperate landscape with shrubs and trees.

Life histories in which the female does not select the place of larval feeding in relation to resource quality

Many life histories have evolved, in many phylogenetic lineages, in which female insect herbivores are relatively unselective in where they oviposit in relation to where larvae will initiate feeding. For example, gypsy moth (*Lymantria dispar*), winter moth (*Operophtera brumata*), and spruce budworms (*Choristoneura fumiferana* and *C. occidentalis*) all lay eggs in late summer, fall, or winter, many months before larvae commence feeding on newly flushing foliage in the spring (cf. Baker 1972; Furniss and Carolin 1977). The first two species oviposit on the bark of trees, and the budworms oviposit on late foliage on which the emerging larvae will not feed.

Applying the hypothesis to this kind of life history involves recognition that an important phylogenetic constraint is that oviposition is separated in time and space from initial establishment of larval feeding sites. Therefore, females are probably unable to evolve with
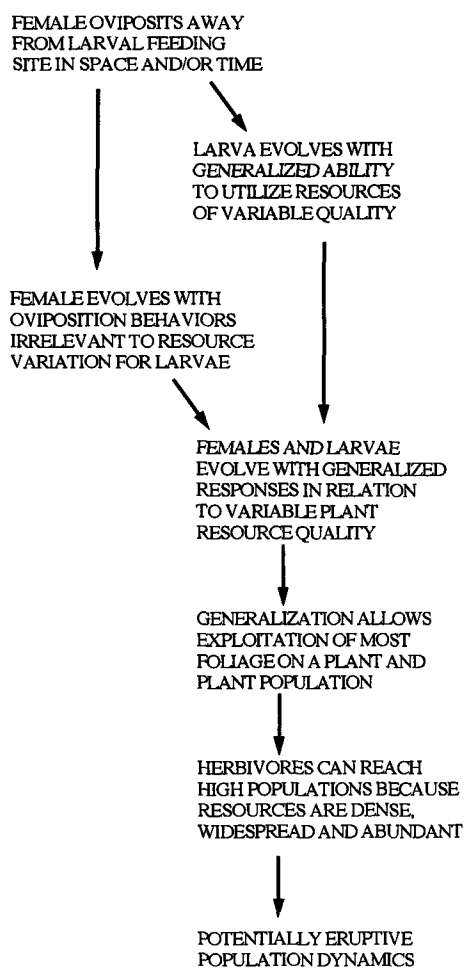
highly selective behaviors relative to resource quality for larvae. As a result, the most important aspect of the adaptive syndrome to minimize this constraint is that larvae evolve with a generalized capacity to utilize effectively almost any food resources they are likely to encounter in the spring. They evolve with a generalist feeding ability. Even if this is restricted to a single host plant species, each larva evolves with a capacity to feed on a wide range of foliage quality. In general, there is no reason to anticipate a relationship between female ovipositional preferences and the performance of her larvae. The preference-performance linkage is likely to be absent.

The emergent properties resulting from this life history type, with its phylogenetic constraints and adaptive syndromes, involve a population dynamics with the evolu-

tionarily based *potential* to be highly eruptive, with outbreaks and heavy defoliation. Such a scenario is linked to the evolved generalized capacity of larvae to consume a wide range of food quality. Thus, sooner or later, populations become high enough to defoliate forests.

Note that the evolutionary approach used in the hypothesis does not address questions about the timing or ecological causes of outbreaks or eruptions, and population declines. It identifies the evolutionary potential for eruptive population dynamics. In a similar vein, ecological factors such as heavy carnivore attack in ecological time may reduce the population dynamics of a potentially eruptive species to the status of an uncommon or even a rare species. Only a detailed evaluation of the bottom-up and top-down forces on insect herbivore

No Preference-Performance Linkage

FEMALE OVIPOSITS AWAY FROM LARVAL FEEDING SITE IN SPACE AND/OR TIME

LARVA EVOLVES WITH GENERALIZED ABILITY TO UTILIZE RESOURCES OF VARIABLE QUALITY

FEMALE EVOLVES WITH OVIPOSITION BEHAVIORS IRRELEVANT TO RESOURCE VARIATION FOR LARVAE

FEMALES AND LARVAE EVOLVE WITH GENERALIZED RESPONSES IN RELATION TO VARIABLE PLANT RESOURCE QUALITY

GENERALIZATION ALLOWS EXPLOITATION OF MOST FOLIAGE ON A PLANT AND PLANT POPULATION

HERBIVORES CAN REACH HIGH POPULATIONS BECAUSE RESOURCES ARE DENSE, WIDESPREAD AND ABUNDANT

POTENTIALLY ERUPTIVE POPULATION DYNAMICS

High Preference-Performance Linkage

FEMALE OVIPOSITS WHERE LARVA WILL SOON INITIATE FEEDING

LARVA PERFORMS BEST ON LARGE MODULES OF HIGH QUALITY

FEMALE EVOLVES WITH BEHAVIORS FOR HIGHLY SELECTIVE OVIPOSITION ON HIGH-QUALITY MODULES

FEMALES AND LARVAE EVOLVE WITH HIGH SPECIFICITY FOR HIGH-QUALITY MODULES

HIGH-QUALITY MODULES ARE VERY LIMITING IN A PLANT POPULATION AND OVER A LANDSCAPE

HERBIVORE POPULATION IS CONSTRAINED TO BE AS STABLE AS HIGH-QUALITY MODULE RESOURCES ARE STABLE

UNCOMMON OR RARE SPECIES ON A LANDSCAPE WITH LATENT POPULATION DYNAMICS
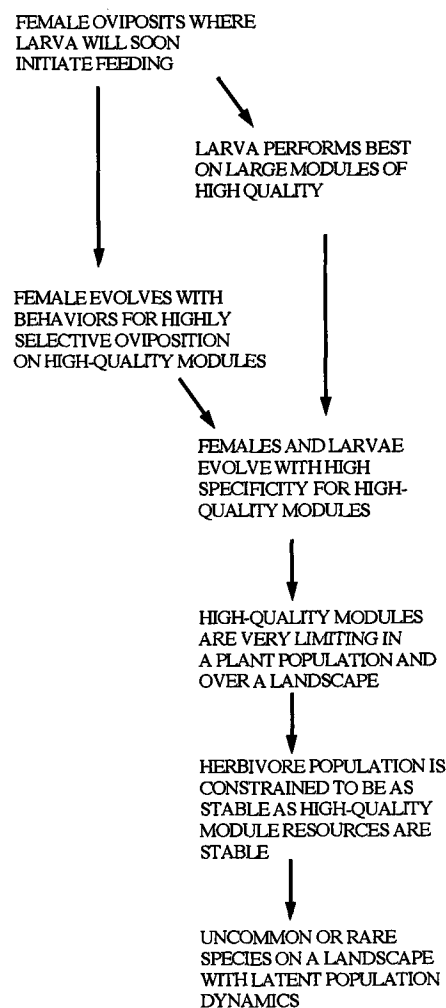
Fig. 1. Predictions of the Phylogenetic Constraints Hypothesis on the train of selective forces acting on species which evolve with no preference/performance linkage, or with high preference/performance linkage.

Table 1. Characteristics of macrolepidoptera known to have shown outbreak population dynamics in the United States and reasons for lack of a tight preference/performance link between ovipositing females and larvae.

FAMILY/Species[a]	Common Name	Oviposition	Lack of Preference/Performance Link
NYMPHALIDAE			
1. *Nymphalis californica*	California tortoishell	Adults overwinter and oviposit in spring	Oviposition of twigs
PIERIDAE			
2. *Neophasia menapia*	Pine butterfly	5–20 eggs in a row	Eggs overwinter and hatch following spring
SATURNIIDAE			
3. *Coloradia pandora*	Pandora moth	5–50 eggs/cluster on needles or bark	Oviposition not specific to foliage, 2-year life cycle. Gregarious feeders.
4. *Hemileuca nevadensis*	Nevada buck moth	Oviposition on twigs in clusters	Gregarious larvae
LASIOCAMPIDAE			
5. *Malacosoma americanum*	Eastern tent caterpillar	200 eggs/mass on twigs	Overwinter as eggs, larvae feed on young foliage. Gregarious feeders.
6. *Malacosoma constrictum*	Pacific tent caterpillar	250 eggs/mass on twigs	Overwinter as eggs, larvae feed on new foliage. Gregarious feeders.
7. *Malacosoma disstria*	Forest tent caterpillar	170 eggs/mass on twigs	Overwinter as eggs, larvae feed on new foliage. Gregarious feeders.
8. *Malacosoma californicum*	Western tent caterpillar	170 eggs/mass on twigs	Overwinter as eggs, larvae feed on new foliage. Gregarious feeders.
9. *Malacosoma incurvum*	Southwestern tent caterpillar	Eggs in masses on twigs	Larvae feed on young foliage gregariously.
LYMANTRIIDAE			
10. *Orgyia pseudotsugata*	Douglas fir tussock moth	150 eggs/mass on female's cocoon	Females need not fly, larvae disperse by wind, overwinter as eggs, larvae feed on new foliage.
11. *Lymantria dispar*	Gypsy moth	750 eggs/mass on trunks and limbs	Females do not fly, larvae disperse by wind, overwinter as eggs, larvae feed on new foliage.
12. *Leucoma salicis* (= *Stilpnotia*)	Satin moth	650 eggs/mass on trees and other objects	Young larvae feed on old foliage, spin hibernaculum, then feed on new foliage.
13. *Dasychira plagiata*			Females with limited movement because of heavy bodies.
14. *Dasychira grisefacter*	Pine tussock moth	300 eggs/mass in loose clusters on needles	Larvae feed, hibernate under bark scales and then feed in spring. Females heavy bodied with limited movement.
NOTODONTIDAE			
15. *Nygmia phaeorrhoea*	Brown tail moth	Eggs in mass on underside of leaf	Females heavy bodied. Young larvae gregarious, feed in fall and spring.
16. *Datana integerrima*	Walnut caterpillar	120 eggs/mass on undersides of leaves	Larvae moult on trunk of tree so female does not select most of foliage in larval diet.
17. *Heterocampa guttivitta*	Saddled prominent	Up to 500 eggs singly on leaves	Larvae migrate frequently from tree to tree.
18. *Heterocampa manteo*	Variable oak leaf caterpillar	Up to 500 eggs laid singly on leaves	Female does not have time to be very selective?
19. *Symmerista canicosta*	Red-humped oakworm	66 eggs/mass on leaves	Larvae are gregarious so feed well away from oviposition site.
DIOPTIDAE			
20. *Phryganidia californica*	California oakworm	60 eggs/mass on leaves and elsewhere	Adults weak fliers and oviposition is nonspecific.
ARCTIIDAE			
21. *Halisidota argentata*	Silver spotted tiger moth	100 eggs/mass on twigs and needles	Unspecific oviposition, colonial feeders.
22. *Halisidota ingens*		Eggs on twigs	Larvae gregarious.

Table 1. (continued)

FAMILY/Species[a]	Common Name	Oviposition	Lack of Preference/Performance Link
23. *Hyphantrea cunea*	Fall webworm	600 eggs/mass on undersides of leaves	Gregarious until last instar.
GEOMETRIDAE			
24. *Anacamptodes clivinaria*	Mountain mahogany looper	350 eggs/mass in bark crevices	Oviposition away from feeding site.
25. *Alsophila pometaria*	Fall cankerworm	112 eggs/mass on smaller twigs and branches	Female wingless, oviposition away from feeding site.
26. *Ennomos subsignarius*	Elm spanworm	70 eggs/mass on twigs	Oviposition away from foliage.
27. *Lambdina fiscellaria*	Hemlock looper	Eggs single or in small groups on moss, lichens, bark on limbs & trunks	Overwinter as egg, feed on opening shoots.
28. *Lambdina punctata*		Eggs single in leaf litter and bark scales	Larvae feed on developing buds and leaves.
29. *Nepytia freemani*		Eggs in small clusters in late summer on needles	Eggs hatch in spring and larvae feed on new foliage.
30. *Nepytia phantasmaria*	Phantom hemlock looper	Eggs laid singly in fall	Eggs overwinter, larvae feed on new foliage.
31. *Operophtera bruceata*	Bruce spanworm	Eggs single in bark crevices, etc.	Female almost wingless, eggs overwinter and hatch in early spring.
32. *Paleacrita vernata*	Spring cankerworm	100+ eggs/mass laid in early spring under bark or in crevices, before foliage is out	Female wingless.
33. *Phaeoura mexicanaria*		160 eggs/mass on needles	Larvae feed indiscriminately on new and old foliage.

[a] Species are listed according to Nothnagle and Schultz (1987) and biological attributes are from Baker (1972) and/or Furniss and Carolin (1977).

populations can reveal the extent to which ecological factors modify the evolutionarily based potential for a certain type of population dynamics. There has certainly been inadequate study of uncommon species and the reasons for their low densities. Many of these species have life histories resulting in the potential for eruptive dynamics according to my hypothesis. But we must await many more detailed studies on such species, including long-term experiments, before the validity of the hypothesis can be tested with uncommon species.

Life histories in which the female selects larval feeding sites relative to resource quality

If life histories include females that are selective on high-quality resources for larvae, such resources may be uncommon and limiting, and may well constrain populations to low-amplitude fluctuations in density, and stable population dynamics. I call these species with latent population dynamics.

Following the hypothesis, the phylogenetic constraints are usually clear. Females ovipositing into plant tissue will commonly require soft plant parts for easy penetration. These are usually found in rapidly developing growth early in the favorable growing season. Hence life histories evolve for synchrony between rapid plant growth

and adult emergence. This is very different from the species already discussed in which immatures overwinter and initial feeding is synchronized with the earliest flush of foliage.

Many kinds of insect herbivore species require rapidly developing plant modules for oviposition and/or early instar development. These include many galling species in diverse taxa such as galling sawflies (Price et al. 1990), galling *Pemphigus* aphids (Whitham 1978, 1980), and some *Diplolepis* cynipids (Caouette and Price 1989), many shoot and cone borers, membracids, leaf-rolling weevils, and many free-feeding tenthredinid sawflies (cf. Price et al. 1990).

Rapidly growing plant modules can be found on young woody plants, especially shrubs, on resprouting shoots after physical damage such as by fire, flood, or storms, and on plants that are artificially or naturally pruned, as with moose browsing in Sweden (Danell and Huss-Danell 1985). All such vigorous growth results after some kind of disturbance; it is therefore patchy in time and space, and frequently a resource with limiting availability. Competition between females for top-quality oviposition sites may well occur in these patches of rich resources, with rapid negative feedback on population size. Both the limiting resources and the competition between reproductive females result in low population sizes, but populations

may be stable over even a decade if rapid growth after disturbance persists that long.

With a phylogenetic constraint requiring oviposition in young plant tissues, an obvious adaptive advantage is that females can select places to lay eggs individually, and eggs can hatch rapidly, soon followed by nymphal or larval feeding at the site selected by the female. Thus, the adaptive syndrome will include highly selective oviposition behavior in relation to successful establishment of feeding by immatures. There will be a strong ovipositional preference linkage to the performance of nymphs or larvae. The evolution of the life history, coupled with the evolved details of female ovipositional behavior, makes these kinds of species very different from those that lack the preference-performance linkage.

The emergent properties resulting from the adaptive syndrome involve highly selective females, with narrowly limiting resources, and competition between females, and a low carrying capacity on the landscape in general even though patches after disturbance may support high populations while regrowth is vigorous. Thus, in natural vegetation, these species are likely to be uncommon or rare at the scale of landscapes, with low amplitude fluctuation in population size.

Application of the hypothesis to species with very different life histories results in very different predictions on their population dynamics (Fig. 1). Some of these predictions can be tested, and will be treated in the next section.

Testing the hypothesis

The hypothesis needs to be tested carefully on the many aspects of the argument. All the evidence cannot be presented in this paper, but it is important to provide some measure of the weight of the evidence. This is because a hypothesis is not accepted or rejected based on a small number of cases but on the relative strength of supporting cases versus cases to the contrary. If my claim is for broad generality, then the hypothesis should be tested in many vegetation types, especially those other than north temperate vegetation. It is in the north temperate that much research on population dynamics has been undertaken and published, forming a literature providing the basic ingredients of life histories and dynamics for the formulation of the hypothesis. However, testing the hypothesis in, for example, desert vegetation or in tropical latitudes is strictly limited by the supply of relevant knowledge from such vegetation types.

For this paper I will limit testing of the hypothesis to three general questions: 1. What are the life history characteristics of outbreak species in North American forests? 2. For high preference-performance species, what is their response pattern to resource heterogeneity? 3. What evidence is there for latent population dynamics in uncommon and rare species?

Life histories of outbreak species

The Macrolepidoptera in North American forests are reasonably well known, if they cause damage frequently enough. Nothnagle and Schultz (1987) listed 41 species reported to have caused visually conspicuous defoliation for at least 2 years in the 20 years of surveys from 1962 to 1981, in the United States of America. This forms the beginnings of a sample I have used for testing the question on life history characteristics of outbreak species. The species were selected objectively and not by me, and they meet the criterion of an outbreak species according to

Table 2. Documented cases of high preference-performance linkage in galling insects.

Insect Species, Order and Family	Module Utilized	Female Preference	Larval Performance	Source
1. *Euura amerinae* Hymenoptera: Tenthredinidae	Young shoot	Longest shoots on very young trees	Highest on longest shoots	Roininen et al. 1993
2. *Euura exiguae*	Young shoot	Long, juvenile shoots on shrub	Highest on longest shoots	Price 1989
3. *Euura lasiolepis*	Young shoot	Long, juvenile shoots on shrub	Highest on longest shoots	Craig et al. 1986, 1989; Preszler and Price 1988
4. *Euura mucronata*	Buds	Buds on long shoots	Highest on longest shoots	Price et al. 1987a, b
5. *Euura* new species	Leaf midrib	Large leaves on juvenile shoots	Highest on longest shoots	Wood et al. 1995
6. *Diplolepis spinosa* Hymenoptera: Cynipidae	Shoot	Long shoots	Highest on longest shoots	Caouette and Price 1989
7. *Pemphigus betae* Homoptera: Aphididae	Leaf	Very young leaves that grow to be large	Highest on largest leaves	Whitham 1978, 1979, 1980

Nothnagle and Schultz (1987). For all 41 species I searched the literature for life history information on the place of oviposition, the time of oviposition, and the place and time at which larvae commenced feeding. This information enabled an evaluation on the extent to which a preference-performance linkage was present or absent.

Sufficient information was found in 33 species of moth, representing 80 percent of the outbreak or eruptive species of Macrolepidoptera in the United States. In every case there is good reason to argue that there is no link between female preference for oviposition sites and larval feeding, so far as the evidence allows evaluation of this relationship (Table 1). In many cases oviposition is separated in space or time, or both, from initiation of larval feeding, so direct contact between the parent and food quality relevant to her larvae is absent. In other cases females may oviposit on leaves but larvae move extensively from this site to feed—they may feed on late foliage one year and early foliage the next—or females may be poor fliers unable to select among host plants or even within host plants. Many species are gregarious, resulting in extensive foraging away from the original oviposition site.

For the available evidence, covering 80 percent of eruptive macrolepidopterans in the United States, the life history information is consistent with the hypothesis. Unfortunately, this life history analysis does not provide any idea of cause and effect relationships among life history characteristics which are needed to test the hypothesis with more rigor. However, the weight of evidence for consistent life history patterns, resulting in lack of preference-performance linkage in these outbreak species, is surprisingly strong in my opinion.

Table 3. Some species of insect herbivore, excluding those in Table 2, which respond positively and significantly to host plant shoot length heterogeneity. All data were collected by the author and associates, except where noted, and were significant at the $P<0.05$ level or the $P<0.01$ level. The r^2 value provides an estimate of the amount of variance accounted for by the regression equation using shoot length classes as the independent variable and probability of attack, or number of attacks per shoot as the dependent variable.

Insect Taxon	Host Plant Species	Locality	r^2
Cynipid Wasps			
1. *Diplolepis fusiformans*	*Rosa arizonica*	Flagstaff, AZ, USA	0.84
Gall Midges			
2. *Rhabdophaga rosaria*	*Salix phylicifolia*	Joensuu, Finland	0.74
Aphids and Related Groups			
3. Wax current shoot galler	*Ribes cereum*	Flagstaff, AZ, USA	0.64
4. *Symydobius oblongus*	*Betula pubescens*	Kevo, Finland	0.76
* 5. *Daktulosphaira vitifoliae*	*Vitis arizonica*	Sedona, AZ, USA	0.81
6. Coccid	*Caesalpinia* sp.	Brazilia-DF, Brazil	0.63
Moth			
7. Amorpha shoot galler	*Amorpha fruticosa*	Lincoln, NE, USA	0.68
Weevil			
8. *Rhynchites betulae*	*Betula pubescens*	Joensuu, Finland	0.75
Sawflies			
9. *Euura atra*	*Salix alba*	Joensuu, Finland	0.91
10. *Euura* petiole galler	*Salix lasiolepis*	Flagstaff, AZ, USA	0.63
11. *Euura* shoot galler n. sp.	*Salix interior*	Urbana, IL, USA	0.73
12. *Phyllocolpa coriacea*	*Salix cinerea*	Joensuu, Finland	0.86
13. *Phyllocolpa excavata*	*Salix pentandra*	Joensuu, Finland	0.51
14. *Phyllocolpa* sp.	*Salix lasiolepis*	Flagstaff, AZ, USA	0.87
15. *Phyllocolpa* sp.	*Populus tremuloides*	Flagstaff, AZ, USA	0.70
16. *Phyllocolpa* sp.	*Salix miyabeana*	Sapporo, Japan	0.65
17. *Pontania* n. sp.	*Salix lasiolepis*	Flagstaff, AZ, USA	0.90
18. *Pontania pustulata*	*Salix phylicifolia*	Joensuu, Finland	0.78
19. *Pontania* sp.	*Salix miyabeana*	Sapporo, Japan	0.71
Psyllid			
20. Leaf roll galler	*Myrcia itambensis*	Belo Horizonte, MG, Brazil	0.79
Cecidomyiids			
20. Leaf fold galls[†]	*Platypodium elegans*	Belo Horizonte, MG, Brazil	0.81
22. *Anadiplosis* nr. *venusta*	*Machaerium angustifolium*	Belo Horizonte, MG, Brazil	0.92
23. Leaf pimple galls[†]	*Eremanthus glomerulatus*	Brasilia, DF, Brazil	0.84
24. Leaf hairy galls[†]	*Eremanthus glomerulatus*	Brasilia, DF, Brazil	0.46
**25. Leaf spheroid galls[†]	*Bauhinia* sp.	Isla Pirapitinga, MG, Brazil	0.80

* Data in Kimberling et al. 1990
** Data from G. W. Fernandes, A. C. F. Lara and L. M. Araujo
† Many cecidomyiids in Brazil remain unnamed.

Response of females with high preference-preformance linakage to resource heterogeneity

This second test of the Phylogenetic Constraints Hypothesis requires detailed studies on female choice of oviposition sites and the performance of larvae at these sites. Some measure of resource heterogeneity is required relevant to within and among host plants. Our research group has discovered repeatedly a strong linkage between female preference and larval performance. Such strong linkage is unusual and our examples perhaps represent the strongest cases known, given the generally poor preference-performance linkage recorded from earlier studies (cf. Thompson 1988; Courtney and Kibota 1990).

The cases we have studied involve galling sawflies in the genus *Euura*, and a gall wasp in the genus *Diplolepis* (Table 2). We can add to our studies the detailed research by Whitham (1978, 1980) on a galling aphid in the genus *Pemphigus*, for a total of seven species in Table 2. In every case the female oviposits exactly where the larvae will feed for the rest of their lives, or in the case of the aphid, the female reproduces parthenogenetically, producing more progeny of larger size on larger leaves. All species remain inconspicuous in a landscape and relatively uncommon, and as a result most are poorly studied except for the reports listed in Table 2.

A broader assessment of pattern of attack by females is possible by measuring shoot lengths and the probability of attack in each shoot length class. A strong and positive relationship is commonly found in many kinds of insects, both in temperate and tropical regions (Table 3). Such patterns are consistent with the hypothesis relating to high preference-performance linkage, but obviously provide less cogent support than the studies in Table 2. Nevertheless, they do provide a much more extensive list of the types of species likely to fit into the group of species with latent population dynamics, although confirmation would take many years of detailed study. In fact the list can be broadened even more by accepting statements in the literature on the vigor of plants that are more commonly attacked by arthropod herbivores. We assembled such a list of 43 cases (Price et al. 1990) involving examples from the Coleoptera, Lepidoptera, Hymenoptera, Homoptera, Diptera, Acarina, and groups of herbivores in different orders. The large majority of these species have females which oviposit where larvae feed, and many of the species were endophagous.

In general, I maintain that there is much evidence to support the Phylogenetic Constraints Hypothesis when applied to species with high preference-performance linkage. More testing is obviously needed especially involving the longer term studies recording population dynamics of these relatively poorly known kinds of species. However, what we do know about population dynamics is treated under the next question to be considered.

Species with latent population dynamics

The third question asked about evidence for latent population dynamics in uncommon and rare insect herbivore species. We have studied two species in some detail that show high preference-performance linkage, *Euura lasiolepis* (Price et al. 1990; Price 1992) and *Euura amerinae* (Roininen et al. 1994). Their dynamics through time are very different and they illustrate how uncommon or rare species may behave in a landscape.

Euura lasiolepis has very predictable population dynamics with fluctuations driven from the bottom up through water availability derived from winter precipitation. Each willow clone maintains a population depending in size on the age of the plant and local water supply. These relationships have persisted for 14 years such that the correlation of densities across clones in 1980 with densities in 1993 is strong and significant. Amplitude of population fluctuations covers only about two orders of magnitude compared to amplitudes of over 3 to 5 orders of magnitude in many outbreak species (Price et al. 1990). The stability and predictability of these populations is remarkable, and is clearly regulated by the supply of vigorous shoots in space and time. Top-down effects from natural enemies are weak and do not change the general pattern of the population dynamics (Price et al. 1990; Price 1992). This pattern appears to be general for many of the *Euura* sawflies, although actual population densities have not been measured over the long term.

An exception to the pattern in *Euura* population dynamics is *Euura amerinae*, which has very predictable dynamics which are, however, locally very unstable (Roininen et al. 1993). Females successfully attack only very young trees of *Salix pentandra*. These are very patchily distributed after disturbance that leaves free mineral soil for colonization. Typically, a young host plant population is colonized in the first 5–8 years of growth, the population increases rapidly, and then declines rapidly, going locally extinct within about 7 years after colonization when trees may be only 12–14 years of age. Natural enemies, again, play no role in shaping the course of population change. The dynamics are driven by bottom-up effects involving host plant colonization of newly available disturbed areas, and a strong aging effect that makes hosts totally resistant by an age of 15 years.

We discuss the probable reasons for these differences in population dynamics in Price and Roininen (1993), and provide additional examples of species with latent population dynamics in Price (1992). Much more research on the population dynamics of other uncommon and rare species is needed before a general case can be made with

assurance.

Discussion

The weight of evidence

I have gone to some length to illustrate the volume of examples which are at least consistent with the Phylogenetic Constraints Hypothesis: 33 species with eruptive population dynamics (Table 1), 7 species studied in detail showing high preference-performance linkage (Table 2), and 25 species which attack long shoots with a higher probability than short shoots, even though long shoots are uncommon and short shoots are abundant on most plants. More examples consistent with the hypothesis are provided in Price et al. (1990) and Price (1992). I have not claimed that the hypothesis covers all cases of eruptive and latent species, but I do claim that the hypothesis helps to account for the basic differences in population dynamics for many species. Thus, citing one or a few exceptions to the patterns described provides only weak arguments against the hypothesis. Rather, a large body of data is needed, such as examples of some 60 species as listed in this paper, showing that an alternative hypothesis has much more explanatory power.

The plant vigor and plant stress hypotheses

The relatively large body of examples of species likely to have high preference-performance linkage, with preference for large plant modules, also supports the Plant Vigor Hypothesis (Price 1991). Large modules commonly occur on young vigorous plant growth, and for various reasons these are favorable for many kinds of insects. In fact, the evidence presented here and elsewhere (Price et al. 1990, Price 1992) adds up to much more support for the Plant Vigor Hypothesis than for unequivocal cases of the Plant Stress Hypothesis (White 1969, 1974, 1976). The mechanisms actually involved in outbreaks of species under apparently stressful conditions for plants have seldom been teased apart for insects attacking the green parts of plants (Mattson and Haack 1987a, b). One advantage of the Plant Vigor Hypothesis is that modules within plants and plants within populations can be readily categorized by measuring module size. Hence data can be accumulated relatively rapidly.

Disentangling evolutionary potential from ecological reality

One challenge for the future is to work with uncommon, non-eruptive species with the life history characteristics producing no preference-performance linkage. Many

such species exist, for example among the forest Lepidoptera (Mason 1987). Why are such species never eruptive? Mason (1987) has argued the case that top-down effects from carnivores keep herbivore populations at low densities. Thus, experiments would be valuable on caged herbivore populations in the presence and absence of their natural enemies. Such experiments should be run for several herbivore generations. Eventually we should discover the extent to which ecological factors override the evolutionarily based potential to be an eruptive species.

Why the chicken comes before the egg

The Phylogenetic Constraints Hypothesis argues that adult female traits, such as morphology and behavior, are the source from which the flow of influences inevitably result in certain kinds of population dynamics. This is because the female chooses the site for oviposition, and she is normally highly mobile, although secondarily flight capacity may be reduced or lost. Therefore, it is the female that can evaluate plant quality variation if necessary on the large scale of a plant population. Larvae have more limited capacity to move freely in a forest or host plant patch. It is the females that have the sensory organs commonly essential in finding hosts and ovipositing on or in the correct hosts. These senses are very well developed and include visual, tactile, and chemical receptors, often used in sequence during the process of finding hosts, finding suitable modules, and then ovipositing. The constraints imposed by the set of receptors a lineage evolves with is clearly illustrated by the many cases in which larvae have a much broader capacity to utilize host plant species than females will oviposit on (e.g. Kogan 1977, Roininen and Tahvanainen 1989, Wiklund 1974, Claridge and Wilson 1978, Smiley 1978, Rausher 1979, 1980, 1983). These two factors, the usually high mobility and capacity to make choices among plants and modules, and the constraints imposed by a battery of receptors adapted to a narrow range of stimuli, make females of prime importance in the identification of phylogenetic constraints.

The role of natural enemies

Remarkably, the role of carnivores in the population dynamics of insect herbivores does not enter into the Phylogenetic Constraints Hypothesis. Generally, I have relegated them to an emergent property, with a possibly important role in eruptive species, but little influence in latent species (Price et al. 1990). However, carnivores can have a strong selective influence on herbivore foraging, and perhaps host plant utilization, with the possibility that female ovipositional choices change in response to selection on immatures imposed by carnivores. I know of no

clearly documented cases of this phenomenon although arguments by Smiley (1978) and Gilbert (1979, 1991) suggest that ecological monophagy may result from heavy carnivore attack experienced on otherwise suitable host plants. If such cases become well established then the hypothesis would have to be modified for some species in which the evolution of female behavior had a top-down component of selection involved.

Common, uncommon, and rare species

The Phylogenetic Constraints Hypothesis provides one avenue into understanding the realm of the differences between common, uncommon, and rare species of insect herbivores. Common species may frequently lack strong linkage between preference of females and larval performance. The strong bottom-up influence on species with tight preference-performance linkage results in very patchy distributions in a landscape and low population sizes in many of the patches. This view contrasts with a more commonly argued perspective that top-down effects are strong on such species, as discussed by Mason (1987). But a general understanding of rare species is poorly developed, as illustrated by the discussion of evidence by Kunin and Gaston (1993). A more focused testing of alternative hypotheses should be explored with some vigor, given the implications for understanding biodiversity and conservation of rare species.

Pest species in agriculture and plantations

The Phylogenetic Constraints Hypothesis may not have much predictive power for understanding agricultural pests and those in plantations. In general, plants in such environments are grown under favorable conditions and are of a uniform age. Hence, even for the highly selective species with tight preference-performance linkage, a large proportion, or even 100 percent, of plant individuals in the population may provide large, rapidly developing modules suitable for attack. The hypothesis does predict that natural enemies may have little influence in such systems. It also predicts that plantation pests may be very different from those in natural vegetation with age-class structure. Species with tight preference-performance linkage are common pests of tree plantations and nurseries, including shoot-boring species in the lepidopteran genera *Eucosma, Rhyacionia, Dioryctria*, and the coleopteran genus *Pissodes* (cf. Price et al. 1990). However, even in plantations populations of these tight preference-performance species should be relatively stable and predictable based on resource supply. Such a case is provided by Mattson's (1980) long-term studies on the red pine cone beetle, *Conophthorus resinosae*. Mattson noted that top-down effects were unimportant in the dynamics of this *Con-*

ophthorus species, showing consistency with the hypothesis. Thus, the hypothesis seems to have some implications for carefully managed systems, by predicting relative importance of bottom-up forces and top-down forces, and the kinds of emphasis in research which are most likely to be rewarding. There is the potential for general hypotheses on population dynamics of insect herbivores in plantation systems.

From individuals to population dynamics

Ultimately, understanding population dynamics depends upon knowledge of the details of life histories, female ovipositional behavior, and the survival of individuals in a heterogeneous environment. What the major scientists involved with insect herbivore population dynamics in the 1950s and 1960s lacked, in my opinion, was the rapid development of many fields starting mainly in the 1970s. These fields include plant-herbivore interactions, evolutionary ecology, chemical ecology, behavioral ecology, biosystematics, and the evolutionary biology of life histories. Now a synthesis of population dynamics with these newer fields is possible and necessary. It provides a powerful blend of analytical perspectives which can tease apart the phylogenetic effects in a lineage, the behavioral contribution to ecological relationships, and for the first time, in my opinion, the conceptual basis to examine thoroughly the relative importance of bottom-up and top-down forces in terrestrial food webs (cf. Hunter and Price 1992). In the last decade this new synthesis on insect population dynamics has advanced rapidly, with a growing number of volumes addressing the central issues in population dynamics (e.g. Barbosa and Schultz 1987; Watt et al. 1990; Hunter et al. 1992; Cappuccino and Price 1995). In the next decade, I predict that hypotheses will be tested with more vigor, and that there will be rapid development toward general theory in insect herbivore population dynamics.

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