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Diprionid Sawflies: Polymorphism and Speciation

Changes in diapause and choice of food plants led to new evolutionary units.

G. Knerer and C. E. Atwood

Sawflies are the more generalized members of the order Hymenoptera that owe their popular name to the well-developed, saw-like ovipositor in the female. The structure is adapted for sawing and boring and for the insertion of eggs into plant material. The adults of the group are easily recognized by the broadly sessile abdomen, so different from the slender waists of their better-known relatives, the wasps, bees, and ants. The specialized habits and instincts of these relatives have never developed in sawflies, despite a long evolutionary history, dating back to the Permian (*1*). But the group presents us with a challenge: its plant-feeding nature has brought it on a collision course with man's interest in his natural resources and its phylogenetic position is of great theoretical value for the study of an order so peculiarly adapted to social life.

The Diprionidae represent only a small fraction of all the sawflies known, but they share the habits of most other leaf feeders. The family is interesting mainly because of the diversity of distinct races or physiological strains that are adapted to specific host plants, and because of the social behavior exhibited by the larvae in aggregations. Both phenomena illustrate various evolutionary mechanisms at work, simultaneously providing examples of newly emerging biologic units and of the origin of some of the most primitive social behavior found in insects.

Diprionid Biology and Behavior

Diprionid sawflies are a well-defined group credited with relatively few morphological and behavioral variations. The family is closely associated with the northern coniferous forest; one subdivision of the family, the Diprioninae, feeds exclusively on the plants of the Pinaceae and Cupressaceae in Eurasia and North America (*2*). All the diprionids are considered destructive, but in North America the greatest damage is done by species introduced from Eurasia. Introduced species temporarily escape their parasites and predators and can thus increase unchecked in the new environment. Few native species reach harmful population densities and the losses they cause do not compare with the losses caused, for example, by the spruce budworm in eastern North America. Outbreaks of native species usually last only a few years before viruses, fungi, and parasites cause a collapse of the infestation (*3*).

There are about 85 diprionid species recognized today, and over half this number belong to the genera *Neodiprion* and *Diprion* (*4*). The latter is widely distributed in Eurasia but is also represented in the nearctic region by the introduced *D. similis* (Hart.), *D. frutetorum* (Fab.), and *D. hercyniae* (Hart.). North America was undoubtedly the center of evolution for the *Neodiprion* species. Few attempts to evaluate the many biological and genetic units have been made and a number of unrecognized species may be disclosed by more intensive studies.

The life cycle of these sawflies is fairly uniform. The females lay eggs in pockets excavated with their saw-like ovipositors in the living needles of conifers. Old needles are preferred and only a single species, *N. swainei* Midd., lays its eggs in the growing needles of jack pine (*5*). The eggs are sealed as they are laid, and are protected by the needle tissue from adverse climatic conditions. The pattern of oviposition is often specific as far as the number of eggs per needle is concerned. *Diprion frutetorum* and *N. abietis* (Harr.) rarely put more than one egg into a needle, whereas *N. lecontei* (Fitch) and *N. rugifrons* Midd. may lay rows of up to 20 eggs in a single pine needle. Intermediate conditions are found in the rest of the species. Subtle differences are shown in the spacing of eggs in relation to one another. *Neodiprion pratti* (Dyar), for example, leaves spaces of several millimeters between the eggs, whereas *N. rugifrons* lays them with ends almost touching. The latter method is also used by *D. pini*

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(L.) and *D. similis*, two species that protect their eggs by a frothy secretion which hardens soon after oviposition (*6*). Females of *D. hercyniae* and *D. frutetorum* scatter their egg complements, but many other diprionids cluster all their eggs on a single terminal branch. This is associated with solitary or gregarious feeding of the young larvae. A more unusual choice for oviposition is made by *Macrodiprion nemoralis* (Ensl.) and *D. virens* (Kl.) on the one hand and a group of *Neodiprion* species closely related to *N. swainei* on the other. All species lay usually a single egg per needle, but while the two *Diprion* species place theirs only 2 to 3 millimeters from the tip of the needle, the *Neodiprion* species lay theirs next to the basal sheath of the leaf (*5*).

The egg and the needle tissue become so intimately associated that the water from the plant influences the further development of the larva. Embryonic development begins soon after oviposition and continues until a distinctly segmented embryo can be recognized (*7*). Further development is suspended at this point in all species overwintering in the egg stage. These include *N. sertifer* (Geoffr.), *N. abietis*, *N. pratti*, and *N. nanulus* Schedl, among others. It has been claimed for *N. sertifer* that the overwintering egg does not represent a true diapause but that desiccation of the host tree and low temperatures during the cold season inhibits further development (*8*). This claim is probably true for *N. sertifer* found in Belgium where mild conditions prevail, but is doubtful for the more coldhardy populations of *N. sertifer* that are found in harsher climates. We found that eggs of *N. pratti* from Virginia hatched in November when they were brought into the 21°C temperatures of the rearing chambers, but we did not succeed in repeating this with Ontario populations of *N. pratti* or *N. abietis*. True diapause seems to take place in the Ontario populations because neither a constant high temperature nor oviposition of eggs in growing trees in spring had any effect on the dormancy of the eggs. They developed normally after exposure to freezing winter weather for 6 to 8 weeks which, incidentally, killed the eggs from the Virginia females. Species in which the eggs undergo diapause therefore have only a single generation a year whereas all other species with or without a prepupal diapause are capable under the right conditions of producing several generations per year.

Eggs swell greatly before hatching thereby forcing the lips of the needle pockets apart allowing the young larvae to escape from the egg. Gregarious species quickly form feeding colonies, young larvae at first eating only the parenchymous tissue, the larger larvae generally consuming the whole needle (*9*). Larvae go through four or more feeding stages in the male and an additional feeding stage in the female. The females become much bigger than the males but are also exposed to predators and parasites for an extra week. Both sexes make their synchronized appearance later in the season because the earlier cocoon spinning of the males is compensated for by a shorter intracoconal development of the females (*10*). Prepupal diapause can last several years in *D. hercyniae* (*11*) or be completely absent in one *N. abietis* strain. Generally it is shorter in northern populations than in southern populations of the same species; southern populations are thus able to avoid high summer temperatures. Diapause induction is controlled by photoperiod acting on the larvae before they spin their cocoons. A short-day regime stimulates *N. taeda linearis* Ross from Arkansas (*12*) to forgo prepupal diapuase while the same reaction is elicited in *N. rugifrons* from northern Ontario by a long day (*13*).

Adult diprionids are sexually dimorphic. The females are relatively weak fliers because of the full complement of eggs they carry on emergence. Males are more slender, better fliers than the females, and usually occur in smaller numbers (*14*). Females produce a pheromone that attracts males, but mating is not essential for oviposition. Unfertilized eggs produce males except in *D. hercyniae*. The adult life span is short and completely devoted to reproduction, which may be accomplished within a day.

Group Effect and Social Evolution

The large and conspicuous feeding aggregations of aposematically colored larvae of certain sawfly species have attracted the curiosity of naturalists for many years. Some authors even included the Diprionidae in the social insects because of the cooperation shown by the larvae (*15*). They argued, without suggesting a direct link between sawfly aggregations and the true social groups, that social behavior could not have developed in the wasps, bees, and ants without there being some indications of such behavior in other members of the order. They suggested that social behavior must have evolved gradually, and that the gregarious behavior of conspecific insects is the first step in this evolution (*16*). The occurrence of social traits, even in otherwise solitary species, is common in Hymenoptera and has made possible the frequent emergence of societies (*17*). Some genetic peculiarity must account for this phenomenon and it is now generally accepted that the haplodiploid mechanism of sex determination fills this role. Hamilton (*18*) has suggested that because sisters in social insects are more closely related to one another than to their mother, altruistic behavior has become advantageous because the genetic homogeneity bestows almost the same fitness to an insect's doing good to close relations as when doing it to itself. This has led to cooperation within colonies but has reduced the individual to a part of a superorganism.

The integration of a diprionid larval aggregation is of a simple nature but its members derive certain benefits from it. Social life cannot be assumed to be advantageous by itself but it seems more than a coincidence that social species are often much more numerous than their solitary relatives. The superiority of higher insect societies is undisputed and has led to the evolutionary elimination of all solitary members in the termites, ants, and honey bees. The advantages of socialization in the sawflies are harder to assess. One example in the tenthredinid genus *Pikonema* is indicative, however. Two populations feed on spruce, but while *P. alaskensis* (Roh.) is common and kills trees, *P. dimmockii* (Cresson) is rare and dispersed. It was shown experimentally that *P. dimmockii* larvae cannot live in groups and get unsettled by contacts with their own kind. *Pikonema alaskensis*, on the other hand, is well adapted to gregarious life and is less alarmed by contact within the feeding group. Other factors may enter the situation but the behavioral difference could account for the contrasting abundance of the two species (*19*).

The physiology and behavior of individuals change when they are removed from the colony. This "group effect" explains the quick death of isolated ant and honeybee workers and is connected with the high mortality of some sawfly larvae when reared singly (*20*). Small larvae of *N. pratti* are not all capable of establishing a feeding site on the needle, but one in three can and the rest join in after the site has been established (*16*). The oviposition pattern of the females reflects the degree of gregariousness in the larvae. The oviposition patterns in the diprionids range from a single egg per needle and sometimes per tree (*D. hercyniae*, *D. frutetorum*) to the row oviposition on a few neighboring needles (*N. pratti*, *N. lecontei*, *N. rugifrons*) (*4*). Big egg clusters are more vulnerable to egg parasites than smaller clusters with regard to their being detected more easily, but such losses are more than compensated for by the greater advantage of large egg clusters to the larvae. Larvae have the best chance of survival in the largest aggregations (*21*), predators and parasites usually being forced to concentrate on the peripheral individuals which have often already been parasitized during earlier stages. The vigorous defensive reactions of *N. swainei* larvae against the predaceous bug *Podisus modestus* reduce the total number lost, especially when the larvae are crowded together (*22*). *Neodiprion sertifer* discourages bird and insect predators by its alarm reactions, the larvae exhibiting a synchronized jerking movement and extruding a large sticky droplet from the mouth (*23*).

Social behavior in other sawflies has evolved even further than the mere formation of larval aggregations. The adults of some species of Argidae in South America, and of the Australian pergid *Perga dorsalis*, guard their eggs and young larvae for several weeks (*24*). This indicates that a higher degree of sociality has become established in that there is rapport between two succeeding generations. But despite these primitive social adaptations in sawflies, the group must remain in an evolutionary cul-de-sac.

The type of food eaten by diprionid larvae appears to play an important role in limiting their social development. Most bees, wasps, and ants consume pollen and macerated insects, two larval foods that are easily transported and stored. A few species of ants and termites that have highly evolved societies satisfy their energy requirements from some vegetative matter by consuming inflated tips of hyphae, the gonylidia, grown in specialized fungus gardens. The more bulky leaves preferred by sawfly larvae deteriorate quickly once removed from the plant. The food is therefore unsuitable for transport and later consumption in a permanent abode, the possession of which is necessary for any highly evolved insect society.

The Systematics of "Hidden Species"

The literature concerning the identification and classification of diprionid sawflies is confusing; it is difficult to assign names with any conviction to even the most common sawflies. The European representatives of the family are perhaps better known than those in North America, where the genus *Neodiprion* is especially enigmatic: apparently identical larval colonies give rise to adults which are demonstrably different and different larvae produce virtually identical adults (*2*). A simple explanation of this problem may be that there are genes in this family that are not expressed in the phenotype during all stages of development. If this is true, then only studies of the genotypes will elucidate the complex relationships among the *Neodiprion* species. The concept of latent or unexpressed genes has been accepted, in principle, for many years, but there is still a strong tendency to identify the members of this group mainly by the characteristics of the genitalia of the females (*25*). The characteristics of the adults are useful in identification when considered in conjunction with larval characteristics, methods of oviposition, food plants, behavior, life history, and distribution of populations (*26*). Cytological studies and studies of egg pigmentation are also useful in the classification of the sawflies and have contributed significantly to our understanding of their phylogeny (*27*).

The history of the European spruce sawfly in North America illustrates some of the problems encountered in a single "species." In 1837, Hartig (*28*) described two sawflies on spruce, identifying them as *Lophyrus polytomum* and *L. hercyniae*. Enslin (*29*) synonymized the latter with the former in 1917, and when a spruce sawfly new to North America defoliated millions of spruce trees on the Gaspé peninsula of Quebec in 1930, the name *Diprion polytomum* was applied to the Canadian pest, on purely morphological grounds (*30*). Parasites of this species were collected in Europe for release in North America during the following years (*31*). Field workers soon became aware of subtle changes in the habits of the "species" since its arrival in North America. The ratio of females to males had changed from the original 1 : 1 reported in Europe to 1200 : 1. In effect, this meant that there had been a change from facultative parthenogenesis to obligatory parthenogenesis, since unfertilized eggs of the Canadian form produced females in almost all instances. The cocoons were now spun belowground in Canada instead of aboveground on twigs as in Europe. But it was not until 1941 that a cytological investigation revealed the existence of two distinct species which had different chromosome numbers (*32*). An intensive morphological study showed differences in adults and larvae between *D. polytomum* and *D. hercyniae*. This not only vindicated Hartig's judgment of a hundred years earlier but also demonstrated that the obligatory parthenogenetic form was the "rare" *D. hercyniae* which had found its way to the New World. The introduced pest was brought and kept under control when a specific virus was accidentally carried in with some parasites and became established throughout the range of the pest species. Thus 11 years had elapsed before a name for one of the most serious forest pests was secured, despite considerable effort on the part of the pulp and paper industry and of the entomologists concerned with the problem. The same urgency of effort has not applied to other diprionid species, and the group remains in taxonomic chaos where the terms "species complexes," "variable" species, and "polyphagous" species hide races of sawflies highly specialized for consuming certain food plants, or clusters of distinct biological units (*33*).

The *N. abietis* complex is a case in point. Its larvae were reported to feed on fir (*Abies*), spruce (*Picea*), Douglas fir (*Pseudotsuga*), and hemlock (*Tsuga*). Field workers noticed biological differences between the larvae reared on spruce and balsam, but the adults from both larval types were said to be indistinguishable (*2*). Studies now show that populations on Douglas fir and hemlock differ to such an extent from all other populations that they must be considered separate units. The populations found on black, white, and Engelmann's spruce have adults that appear identical and striped larvae that are impossible to tell apart (Fig. 1a). The populations on the firs are more distinct. The white fir sawfly on *Abies concolor* in California is very different from the eastern strains, and can readily be recognized in all stages, though the larval pattern of late instars somewhat resembles that of the spruce strains (Fig. 1c). Balsam fir is the host of two distinct races, one with small individuals and with dark larvae and adults (Fig. 1b) and another that is larger than the dark individuals and indistinguishable at sight from the spruce strains (Fig. 1d). The *N. abietis* complex therefore falls into three visible subdivisons: a population of small dark insects on balsam fir; a large, distinct form on white fir, and a conglomerate of all the spruce strains together with the larger balsam form. Biological studies have confirmed the validity of the preliminary diagnosis and have supplied the critical information on the degree of distinctiveness of all the other strains (*34*).

Seasonal Isolation

All the populations of the *N. abietis* complex that have been studied have different seasonal appearances. The white fir strain is adapted to the California climate in that the eggs are dormant during the winter, and the larvae hatch in early spring and complete the last feeding instar quickly. The prepupae undergo extensive diapause until the adults finally appear in late fall. In all other strains the eggs, larvae, and pupae have different developmental rates (Fig. 2). The larvae hatch either early or late and adults emerge with or without a prior diapause. Various combinations of these different developmental rates account for the different seasonal appearances of the strains, and such differences do not appear to be solely adaptations to climatic conditions. Very different phenologies are observed especially where populations are sympatric. The two balsam strains occur together in Ontario. The dark larvae of the smaller form hatch early in spring, feed until June, and the adults emerge without delay in July. This strain is therefore called the "early balsam" strain and differs from the "late balsam" strain not only in its larval color pattern but also in its different developmental rate that isolates it from the late balsam strain very effectively (Fig. 2). But divergence into different units does not stop here. Hardly a single population has been studied in any detail that does not show some peculiarity which sets it apart from similar populations in a different locality. An isolated population of the early balsam strain, for example, was found near Toronto at the southern edge of the host's distributional range in this area. The population appeared more robust and the larvae more striped than usual but measurements of the head did not indicate any difference in female size. Dissection of the females, however, did establish a 50 percent average greater fecundity of the isolated population. The variations in the late balsam strain are more pronounced. An outbreak of *N. abietis* in Nova Scotia in the last few years defoliated balsam fir, white spruce, and black spruce. The identical looking adults had staggered emergence times that might have been acting as an isolating mechanism. One strain identified as the late balsam strain took 2 months longer to complete development than the similar strain from Ontario when both were tested under identical laboratory conditions (*34*).

Phenological differences have developed in other *Neodiprion* races adapted to specific food plants. *Neodiprion nanulus* occurs in northern Ontario on jack pine and red pine, respectively. There is no suggestion of any morphological differences in the adults or larvae, but the northern Ontario populations on jack pine show a faster developmental rate than the populations on red pine. The differences may reflect environmental adaptations rather than constant physiological characteristics. Egg pigmentation from the two types indicate differences with some overlap, perhaps caused by cross-feeding. The information now available points to incipient host races but more data from the field are needed to solve the problem (*25*).

Geographic Subunits

A different situation exists in *N. pratti*, a widely distributed complex that feeds on a great variety of pines. Three geographic subspecies have been proposed (*2*). The northwestern *N. pratti banksianae* has striped larvae and feeds on jack pine. The southern *N. pratti pratti* also exhibits a striped larval pattern but occurs on a variety of pines found in Virginia and the Carolinas. *Neodiprion pratti paradoxicus*, which has spotted larvae and feeds on jack and pitch pine, occurs between the two extremes. Large transitional

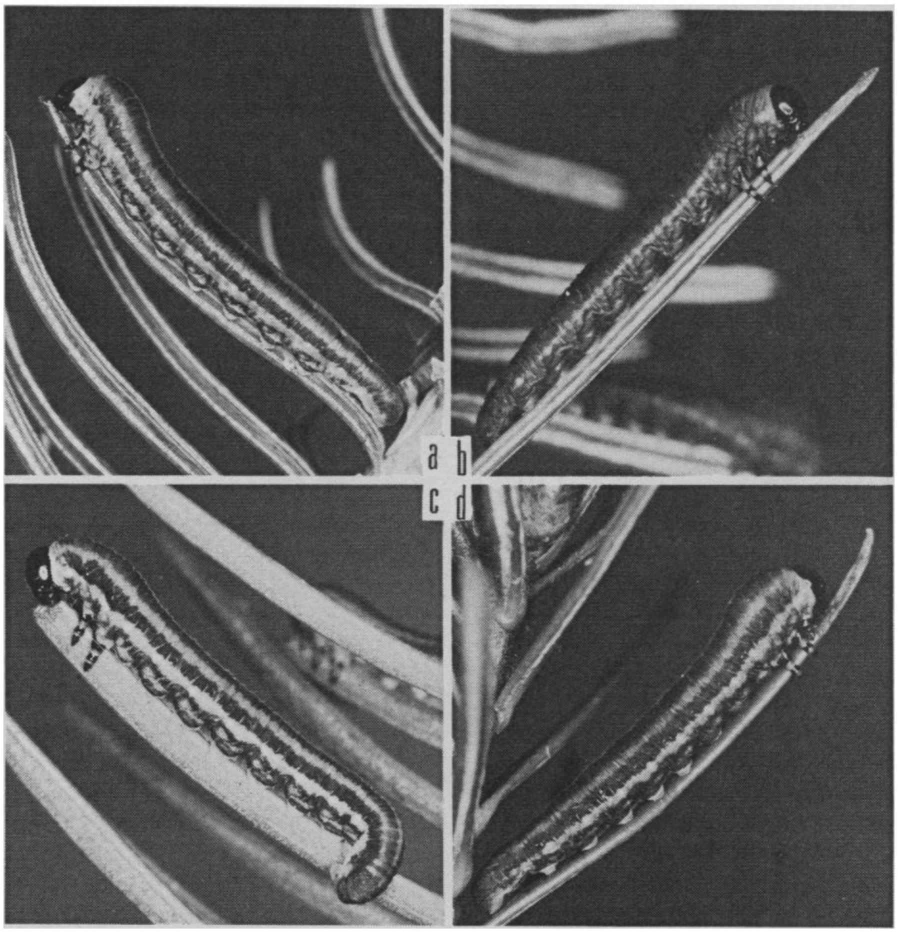

Fig. 1. Mature larvae of different strains of *N. abietis* on their normal food plants. (a) White spruce strain from Alberta eating whole spruce needle. (b) Early balsam strain from Ontario, skeletonizing balsam fir. (c) White fir strain from California, eating whole needle of white fir. (d) Late balsam strain from Nova Scotia, skeletonizing balsam fir.

zones between the populations are reported in which a great diversity of larval patterns is seen. It is not impossible to rear all three larval types and their intermediates from the progeny of a single female, and the same is true for another subspecific criterion, the color of the female head. This makes it virtually impossible to delineate meaningful units by the use of these characters. Identification of the subspecies by means of their food plants is often equally meaningless because larvae can feed on a great variety of pines, and females seem to oviposit on most pines available to them, except the white pine group. Physiological differences are present within the species but prepupal and egg diapause characteristics change along a north-south cline without regard to any possible taxonomic division. The shift in adaptation to temperature is associated with cold-hardiness of these strains. Eggs collected in Ontario needed about 2 months of cold weather before embryonic development was resumed and the larvae hatched. Eggs collected in Virginia developed without exposure to cold in the fall but eggs from this population perished when exposed to an average Ontario winter. Many more examples of similar differences are known from other complexes, but not enough data are available to elucidate all their characteristics.

Host Colonization and Host Defense

The association of a sawfly group with a group of closely related plants may indicate a coevolution of the insects with their hosts or may indicate a purely physiological association (*33*). The narrow restriction of the Diprionidae to the families Pinaceae and Cupressaceae reflects the insects' attempts to utilize the similar physiology of these plants to their own advantage. Conifers have evolved a most sophisticated chemical defense system of repellents and toxins that discourages all but the most specialized plant feeders that have the biochemical capabilities to render these substances harmless (*35*). The acquisition of such an enzymatic detoxification mechanism could establish an insect on one of these protected plants, and mutants from this insect might be able to colonize all other closely related hosts (*36*). Because of the pine-feeding nature of most Diprionidae it is logical to conclude that *Pinus* was the original host before other genera were invaded (*2*). Jack pine especially is the host of a number of monophagous or oligophagous species—*N. rugifrons, N. swainei, N. maurus* Roh., and *N. nigroscutum* Midd.—and is even acceptable as larval food to all strains of *N. abietis* which are in nature not even associated with that plant genus and whose females never lay eggs on *Pinus*. Red pine and white pine cause high mortality among the larvae of these species, but not in polyphagous *D. similis, N. sertifer, N. pratti*, and *N. lecontei*.

The physiology of the host is of the utmost importance to the survival of the Diprionidae, for weakened or desiccated trees are attacked more successfully than healthy ones (*37*). Damages to plantations by *D. pini* and *N. sertifer* were related to a prolonged drought period prior to the outbreaks in Holland in 1951, and mass infestations of *N. sertifer* occurred in places with abnormally low water tables in Austria (*38*). Physiologically weakened trees are especially attractive to the ovipositing females which often select needles having a very narrow range of water content. Larval mortality of *D. pini* was much higher in well-watered stands than in drier localities and application of fertilizers raised the tree resistance significantly against these insects (*39*). Very vigorous trees possessing leaves with high water content are virtually ignored by egg-laying females; females have a predilection for the same weakling trees from one generation of sawflies to the next. Copious resin flow from the oviposition scars greatly reduced the number of viable eggs when *N. hetricki* Ross oviposited on slash pine instead of loblolly pine (*40*). Species with row oviposition risk greater losses of eggs or larvae by selecting unsuitable needles, therefore it is not uncommon to find empty test slits in many needles where females have attempted oviposition but have failed (*41*). The most curious behavior that is well worth more intensive study is exhibited by *N. nigroscutum*, a species laying a small number of eggs on jack pine. The females gouge out abnormally large pockets that injure the central vascular bundle of the leaf which thereupon dries up beyond the

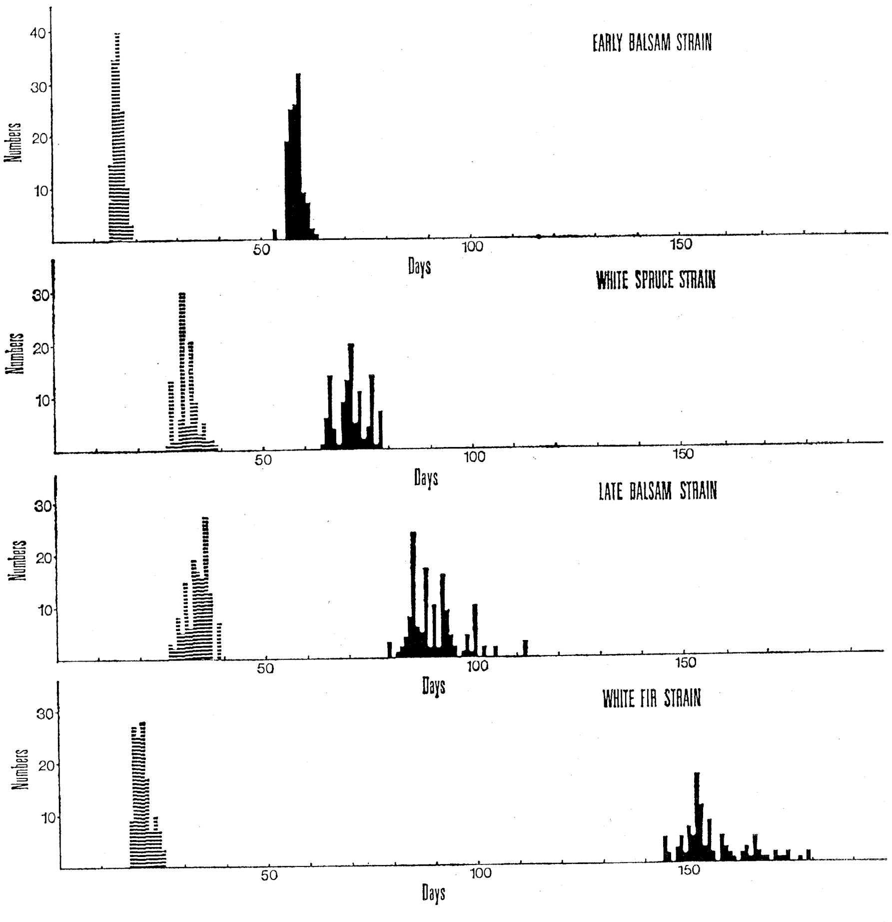

Fig. 2. Differences in larval hatching (striped) and adult emergence (solid) of the various *N. abietis* strains reared under identical conditions.

first pocket, thus killing all but the most proximal egg (*42*).

The amount of resin flow caused by the feeding of larvae is important; newly hatched larvae often drown in the sap oozing from the feeding scar. The mortality of the first instars of *N. nanulus* and *N. abietis* on red pine was related to the turgor of the foliage offered to them, but on several occasions it was noticed that some groups of larvae started several feeding sites in succession before forming a permanent aggregation. The resin flow from the first few scars may have forced the larvae to move on but the net effect was that most of the sap drained from the needle, which could then be consumed. Survival techniques of this kind are also known from caterpillars of various Lepidoptera and are well illustrated by the small monarch butterfly larvae that chew halfway through the petiole of the milkweed leaf; this results in a great reduction of the latex at the actual feeding site (*43*).

Toxins and Phytohormones

The presence of certain secondary chemical substances or allelochemics in pines requires certain metabolic modifications on the part of the larvae, depending on which pine species they feed. The loblolly pine and long leaf pine are taxonomically somewhat remote from the northern jack pine and thus differ in their allelochemics; this probably explains the lack of success encountered when the larvae of *N. taeda linearis* and *N. excitans* that normally feed on the loblolly pine and long leaf pine were put on the northern jack pine.

Further detoxification mechanisms were required before the pine-feeding sawflies could become established on other coniferous genera, especially the spruces and firs. These plants also contain allelochemics that affect the growth, health, and metamorphosis of the insects that feed on them (*35*). Balsam fir proved singularly toxic to the pine-feeding larvae of *Neodiprion* spp. when these were transferred to this particular host. It is perhaps not surprising then that juvabione, a mimic of a juvenile hormone of certain bugs, has been extracted from the wood of balsam fir and there is a growing list of phytohormones found in a great variety of gymnosperms (*44*). The mimetic substances are sometimes very specific, interfering with the development of only a small group of related insects. They are also very potent, being effective in lower concentrations than the natural hormone (*45*).

This phenomenon accounts for some of the experimental results obtained with the various food strains in the *N. abietis* complex. When newly hatched larvae of the early and late balsam strains were put on balsam fir, spruce, and jack pine, the larvae survived on all three hosts almost equally well and appeared to grow on spruce somewhat better (Fig. 3). But the same experiment resulted in a complete mortality of the white and black spruce strains when they were placed on the fir foliage. The small larvae behaved normally on this food for the first few days, forming feeding aggregations, eating, and voiding frass. Within a week, larvae had wandered away from the feeding site and died without one individual having molted into a second instar. The white fir strain proved ill-adapted to all eastern food hosts offered. The larvae not only died when put on balsam fir but showed extremely high mortality on jack pine too (Fig. 3).

Biochemical adjustment by the two balsam strains has been accompanied by a behavioral modification in the larval feeding pattern. The needles are skeletonized and only the peripheral portion is eaten. It was thought at first that the high concentration of allelochemics in the central vascular bundle of balsam foliage was avoided by this behavior, but the larvae retained the same feeding pattern on spruce and jack pine foliage. The trait has obvious selective value and is probably carried by a single dominant gene, because all

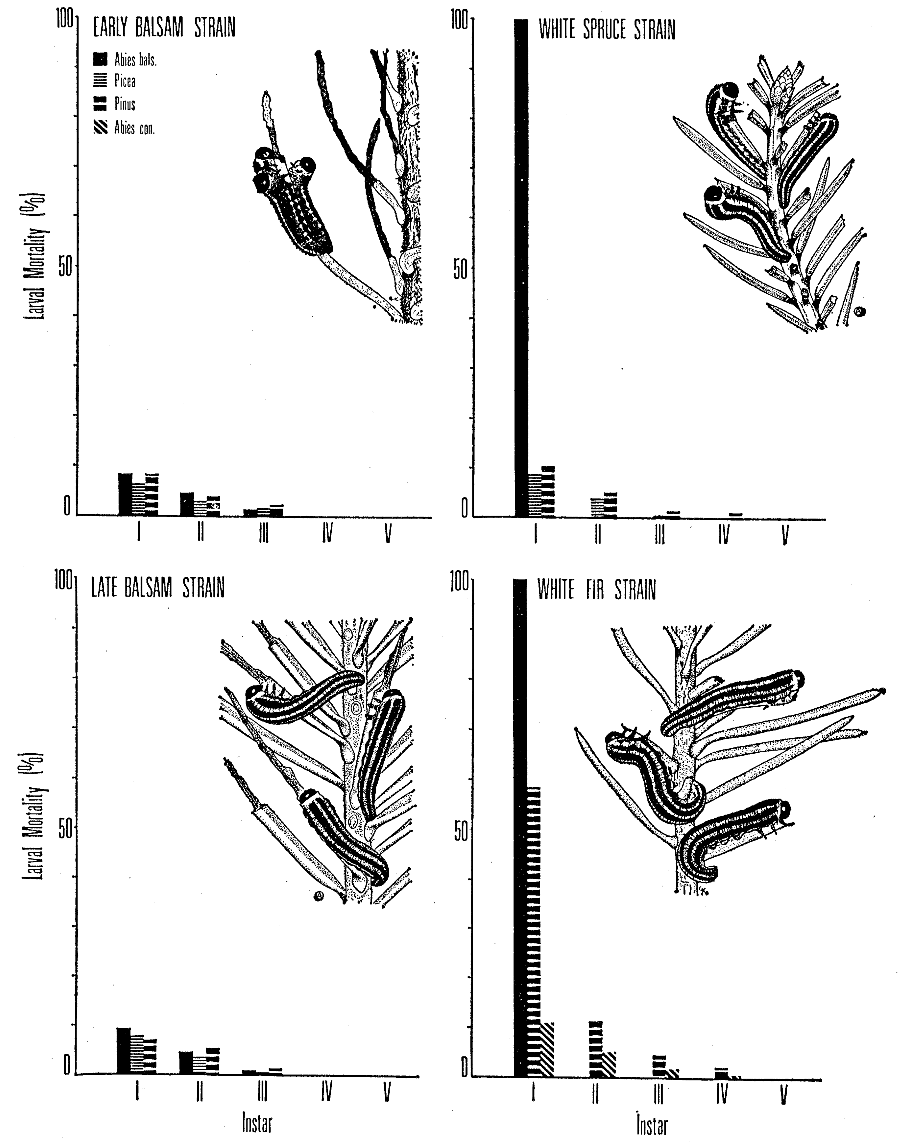

Fig. 3. Larval mortality and feeding patterns of four *N. abietis* strains on a variety of conifers.

hybrids between the spruce and balsam strains retain the trait when feeding on the appropriate foliage (Fig. 4). The feeding of the hybrids is of the "whole leaf" pattern on all foliage tested except balsam fir. This host causes the hybrid larvae to switch to the skeletonizing pattern which is reversed once more when the larvae are returned to some other foliage (*34*).

The larval survival experiments clearly indicate that balsam fir can only be used as a niche by the most specialized strains of the *N. abietis* complex. Full genetic adjustment must have taken some time to achieve and is evidently under polygenic control. Hybridization experiments, however, suggest that genotypic alterations have not been on a large scale. This is borne out by the hybrids from closely related parents, for example, the late balsam strain crossed with the spruce strains. Survival of the diploid larvae was exceptionally high on the balsam foliage and both larvae and adults seemed vigorous and robust. Crosses between the other strains showed higher mortality of the resulting hybrids on balsam or abnormally long developmental rates. Cytoplasmic factors are indicated in the inheritance of some of the traits by the significant differences in survival by the hybrids when the sex of the contributing strains was reversed. That some of the crosses were successful came as a surprise, especially between the very different late balsam strain from Nova Scotia and the white fir strain from California. Both larvae and adults showed the effects of genetic maladjustment by their extremely slow growth and their stunted appearance (Fig. 4).

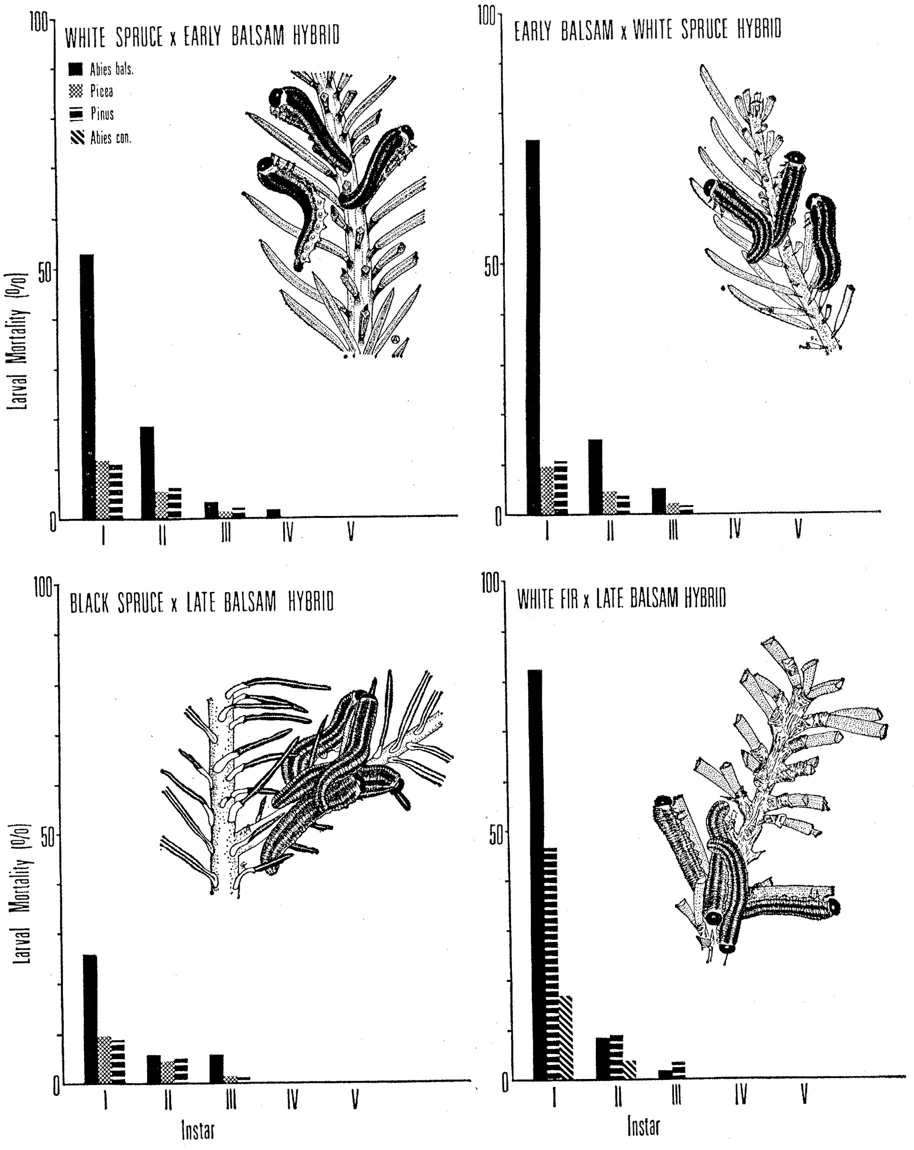

Fig. 4. Larval mortality and feeding patterns of some *N. abietis* hybrids (female is first name of the cross). Striking differences not only exist between hybrids of different strains but even between the same cross if sexes are reversed.

Host Preferences

Fieldworkers have been puzzled by situations where some larvae of the *N. abietis* complex were found on a balsam fir that grew among the lower branches of a larger spruce (*25*) or vice versa. It was invariably observed that one host was nearly defoliated whereas the foliage of the other tree remained untouched. The avoidance of balsam fir by the spruce strain is explained by the high toxicity of balsam fir to these larvae. There is no obvious reason why the larvae of the balsam strain should not feed on spruce foliage, especially when the branches of the two plants interlace. Newly hatched larvae of the balsam strain actually prefer spruce over balsam when given a choice of several host species, but once habituated to a particular foliage they rarely leave it during later feeding stages.

In the field, little choice of food plants is available to the young larvae that find themselves on the needles selected by their mother many months before. The onus of recognition and selection of the right food therefore rests with the ovipositing females. Experiments with newly emerged females of all *N. abietis* strains showed a range of host constancy. Most females oviposited on their traditional hosts in a "choice" situation, but results varied when only foliage of other kinds was available. The white fir strain, for example, laid many eggs in the unfamiliar balsam fir, whereas other strains often had difficulties with the mechanics of laying on plants they were not used to. The most rigid host selection was found in the three *N. abietis* strains found in Nova Scotia. All females accepted only their respective hosts, balsam fir, black spruce, and white spruce, for oviposition and died after several days with their full complement of eggs if the normal host was not offered. Preimaginal conditioning was not a factor in either the pure strain or hybrid females. Host selection has a genetic basis and is apparently under monogenic control. Hybrids from the balsam strains crossed with spruce strains selected balsam fir for oviposition thereby suggesting that the allele for balsam selection is dominant over its allele for spruce selection. The implications of this trait on the hybridization potential of the strains must be of great magnitude and must also play a decisive role in the evolution of food races in this complex.

Emergence of New Biologic Units

The genus *Neodiprion*, with its many closely related species and numerous subdivisions of these species into geographic and host-plant races, provides an excellent illustration of the evolutionary pattern in this group (Fig. 5). Two recurring themes show constant variations in the genesis of new species: the adaptation of a population to a new plant host with the resulting spatial isolation of the two related types, and the modification of developmental times, including diapause in the egg and prepupal stages, which causes a subsequent temporal isolation of the new population from the old. Numerous examples of both mechanisms enable us to reconstruct the way in which new units probably emerge. Completed speciation is best illustrated by a group of species related to *N. swainei*. At least three species are involved: *N. swainei* on jack pine and *N. hetricki* on pond and loblolly pine, both species having a single generation per year; and *N. excitans* on several southern pines having multiple generations per year. A change in overwintering habit from the prepupal to the egg stage effects temporal isolation with complete efficiency without involving geographic separation (*5*). This process has been shown in *N. sertifer* to be reversible (*38*) and would be most favorable during and after periods of glaciation. For instance, *N. hetricki* could have arisen from an ancestor with the *swainei* pattern of development and oviposition. Its developmental chronology in the south during the glacial compression then changed to overwintering in the egg, and the larvae began to feed on southern pines when the jack pine followed the retreating ice cap (*5*). This evolutionary situation may have been repeated several times during the cycles of climatic changes when bursts of physiological variation led to colonization of the southern pines by this group and its subsequent differentiation into distinct species during periods of retrenchment.

Species with confirmed polyphagy usually have a wide distribution and ill-defined subdivisions, because the lack of reproductive isolation prevents the formation of distinct genotypes. The three subspecies of *N. pratti* seem to fall into this category. Despite the criteria by which they can be distinguished morphologically and physiologically in the larval and adult stages, no clear separation of the units can be accomplished when individuals representing all the varieties within the species are considered. It becomes apparent that the same characters are not consistently associated with the same geographic units and the zones of transition do not contradict the clinal nature of these characters. The populations from the northern and southern extremes of the range are biologically quite different, but cannot be considered taxonomically distinct unless external and internal factors effect the genetic isolation of the three varieties and the removal of their transitional populations. Selection pressure has had some effect on *N. sertifer*, the most widely distributed diprionid sawfly known. Two types are recognized, the common lowland race and a localized mountain race in the Swiss Alps. Both races differ in their overwintering stages and certain morphological characters in adults and larvae (*38*).

A similar vertical distribution appears to play a decisive role in the fragmentation of *N. fulviceps* in California. Three isolated populations were found, one near Willits and two at different elevations on Mt. Shasta. All three populations overwinter in the egg stage and the larvae are able to feed on ponderosa, Jeffrey, and Monterey pine. But color and spacing of the eggs in the three localities was different as was the hatching time of the larvae, because the population at the lowest altitude with the warmest climate had the latest hatching date. Even larval size and color pattern were so consistently distinct that little doubt remains that three separate genetic units were encountered (*46*).

Monophagous species may be restricted to smaller areas by virtue of the distribution of their single host. Any mutation giving rise to forms with aberrant feeding habits might result in spatial isolation of the two populations if the host trees occupied different geographic areas or habitats. Two incipient races have been reported in *N. nanulus*, one race feeding on jack pine and the other on red pine, but no morphological differences have been detected in the adult populations (*25*). Adaptations of these races to their host plants have already led to some physiological polymorphism since oviposition choice is not influenced by preimaginal conditioning (*47*) and developmental differences may already separate the two populations completely.

Splitting the N. abietis Complex

Nowhere has the combination of specific hosts and different developmental times been deployed with greater abundance than in the *N. abietis* complex. It seemed at times that every population investigated had its own rate of development. These differences

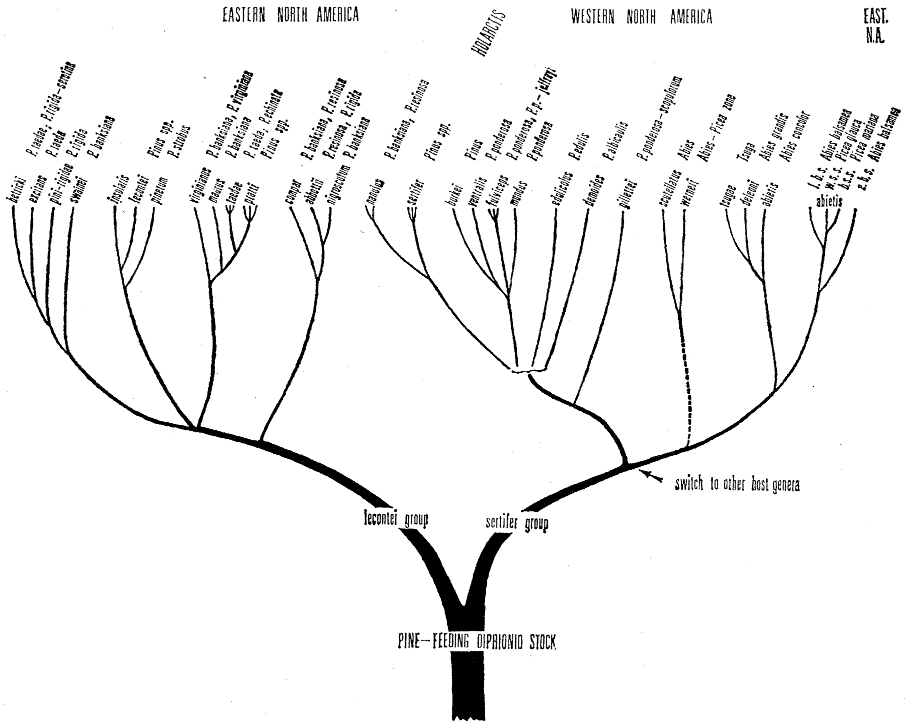

Fig. 5. Family tree of the genus *Neodiprion* showing the known species and subunits with their coniferous hosts. [Based on Ross (*2*)]

were not mere adaptations to the various climates encountered across the continent but they served positively as isolating mechanisms. This was illustrated by sympatric populations of *N. abietis* strains in Nova Scotia and Ontario. In the latter province both early and late balsam strains are found in close proximity and sometimes on the same tree. Only a perfect isolating mechanism could prevent hybridization in this situation and nothing less was found in July 1970 in the vicinity of Minden, Ontario. A medium-sized balsam tree was found to bear several feeding aggregations of small larvae of the late balsam strain while red patches higher up in the crown betrayed the previous activity of the early balsam strain whose larvae had already departed to spin their cocoons. Both the short larval hatching period and the time at which adults emerge in the late balsam strain are retarded considerably so that there is a time lapse of 6 to 8 weeks between the flight periods of the two strains. In addition, the two strains are isolated ecologically in that they choose different oviposition sites. The early balsam females prefer to oviposit and perhaps mate near the top of the balsam tree whereas the late balsam strain more often chooses the low branches for this purpose, even those sweeping the ground.

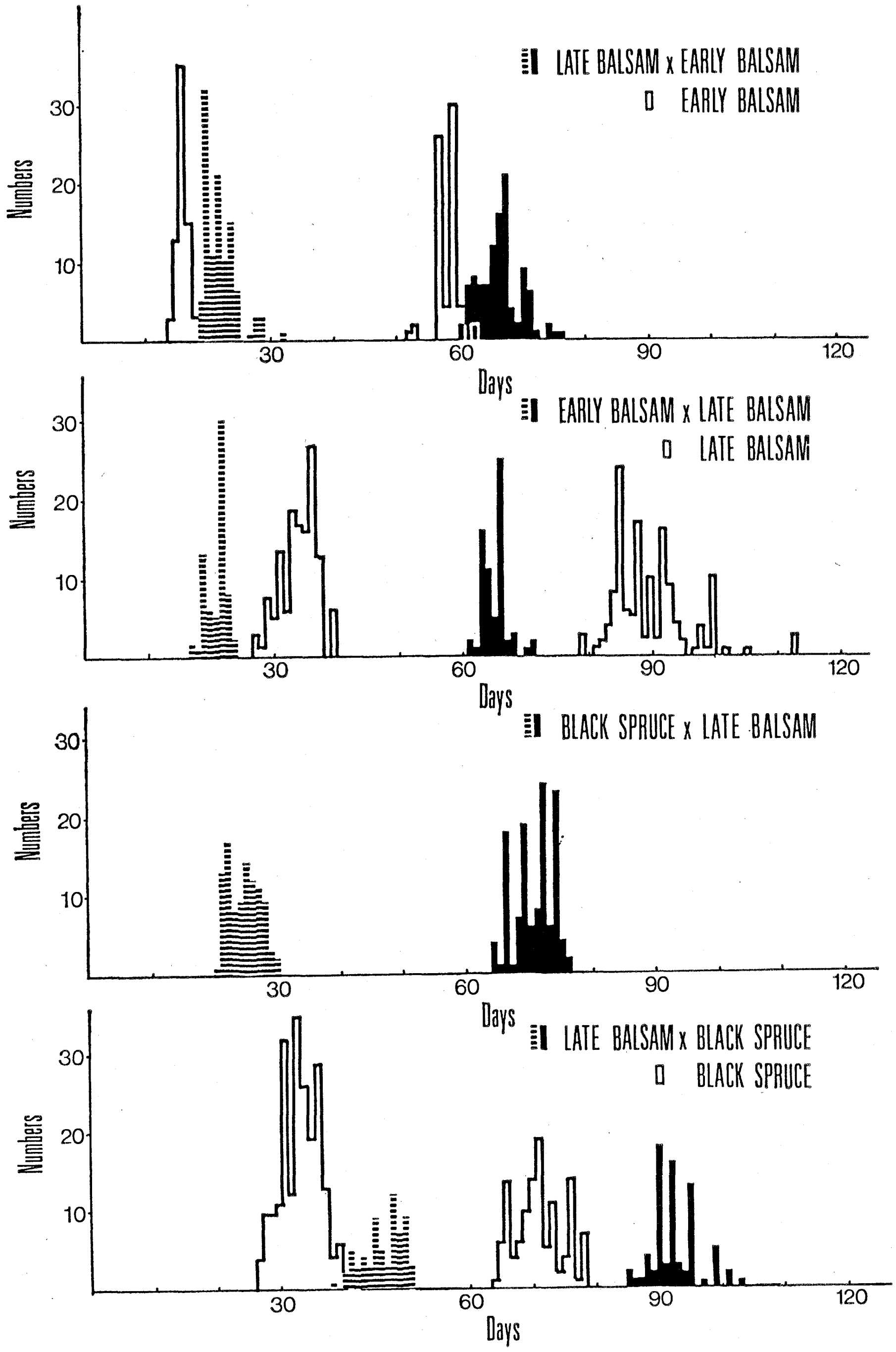

Fig. 6. Inheritance of developmental rates in hybrids of *N. abietis*. A reversal of the sexes of the first cross was without effect. A cytoplasmic factor seems to be responsible for the marked shift in emergence of the second pair of crosses.

An outbreak of *N. abietis* in Nova Scotia also occurred in 1970 and three food strains were found existing sympatrically on balsam fir, white spruce, and black spruce. The differences in the developmental rates of the adults were not as pronounced as they were in the two balsam strains observed in Ontario, but this was probably because the ecological isolation of the hosts played an important role. On balsam, only the late balsam strain was present and this strain took 2 months longer to develop than its Ontario equivalent when both were reared under exactly the same laboratory conditions. The longer time needed by the late balsam strain was only partly a response to the maritime climate of Nova Scotia; it also allowed the white spruce strain and the black spruce strain to stagger their flight periods prior to the emergence of the balsam strain.

Such a situation could have been caused by a population of the balsam strain exploiting two other hosts conveniently present in the area. But in this instance, rigorous experiments dispelled this possibility and established the presence of three discrete units, although no apparent differences were noted in the larvae or adults. The immature stages showed little mortality when reared on the host they were found on, a sign that no spruce/balsam hybrid could have been involved, because mortality of spruce strains on balsam is at least 50 percent (Fig. 4). Larvae were then switched to the alternative hosts and it was found that both the white and the black spruce populations had no survivors on balsam, thus running true to form for these strains. Finally the newly emerged females were given a choice of trees to oviposit on and the selection of the host was reasonably accurate. If the preferred host was removed, no oviposition took place at all and most females died with their full complement of eggs. These tests established the sympatric occurrence of three extremely similar looking races that remain reproductively isolated by a combination of rigid host preference, not quite perfect seasonal separation, and perhaps other factors not obvious to human investigators but essential to the insects.

Evolutionary Trends

How was the evolution of these strains initiated? We agree with Ross that the *N. abietis* line had a pine-feeding ancestor before it was carried into a new adaptive zone. The experiments that determined the survival of larvae on various host plants imply that the first change in food preference was made to spruce and not to the true firs (*Abies* spp.) as has been suggested (*2*). The larvae then moved from spruce to the more demanding hemlock (*Tsuga*), Douglas fir (*Pseudotsuga*), and the true firs, including the most toxic species, *A. balsamea*. Mutant genotypes with the specific detoxification mechanism against the allelochemics of the balsam fir and the neural adjustments for the apparently adaptive skeletonizing feeding pattern on this host suddenly found themselves on a previously little utilized food plant. At least two invasions of balsam fir have been successful. The early balsam strain undoubtedly represents the first colonization of this host since it has had time to diverge considerably from all the other members of the *N. abietis* complex. The acceleration of overall development opened up the same niche for a late arrival whose relatively unmodified developmental rate and appearance betrays its great affinity with the spruce strain. Ecological isolation is important in the evolution of insect populations and it has been repeatedly pointed out that the favored host not only provides food but also shelter, mates, and enemies (*48*). A host is an island surrounded by a sea of different plants, harboring other creatures that are ill-adapted to enter this microcosmos and are repelled by the host's defense.

The Senita cactus of the Sonoran desert embodies such an evolutionary island populated solely by *Drosophila pachea* to the exclusion of all other species of the genus occurring in this region. The *Drosophila*-cactus relationship is based on the ability of *D. pachea* to tolerate the alkaloids contained in the cactus which have proved lethal to all other drosophilids tested. The toxicity of the plant supplies the only apparent isolating mechanism because seasonal isolation can hardly be a factor in these flies (*49*).

Introgression between sympatric strains of *N. abietis* is obviously rare in nature despite the ability of such strains to hybridize in captivity. The ecological and temporal isolation can perpetuate the integrity of the strains under normal conditions. Unusual climatic stress causing the breakdown of seasonal differentials can lead to interbreeding of the strains involved but the consequences are slight. The hymenopterous method of sex determination results in an F_1 hybrid generation consisting only of females that later emerge between the flight periods of the two parent populations; the F_1 hybrids can then only produce an F_2 generation consisting of hybrid males, unless they find a mate from an overlapping parent population in which case they quickly lose their new genetic entity (Fig. 6). Hybrids between balsam and spruce strains have the additional problem of surviving the immature stage when the larvae find themselves on balsam fir. But this is one of the consequences of evolutionary processes: an overwhelming majority of F_1 females select balsam for their egg laying.

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50. We thank the many officers of the Canadian Forest Insect Survey for information and help in collecting material. Supported by National Research Council, Ottawa, and the Canadian National Sportsmen's Show Conservation Fund, Toronto.