TAXONOMIC STATUS, BIOLOGICAL ATTRIBUTES, AND RECOMMENDATIONS FOR FUTURE WORK ON THE GENUS *LYGUS* (HETEROPTERA: MIRIDAE)

By Thomas J. Henry and John D. Lattin[1/]

Species of Lygus, frequently called lygus bugs, are the most important agricultural pests in the plant bug family Miridae (Heteroptera). The tarnished plant bug, Lygus lineolaris (Palisot), occurring over most of North America, is a pest of cotton in the Southern United States. In the Western United States, several species attack alfalfa and cotton. Because of the severe damage these plant bugs inflict, an extensive search has been implemented by the U.S. Department of Agriculture and cooperating agencies for natural enemies, especially nymphal parasites in the wasp family Braconidae. This report is an overview of the taxonomic status of the genus Lygus to help biological control researchers better understand the taxonomy of Lygus and the taxonomic problems related to controlling this pest group.

The plant bug genus Lygus in North America contains several economically important species. They feed on a variety of crops and native plants. Some species are widely distributed and broadly overlap the ranges of others. Great morphological variation in adults often makes positive identification difficult. At least some species of Lygus are parasitized regularly by Braconidae, chiefly in the nymphal stages. Positive identification of Lygus nymphs except in rare instances is not now possible. The variations caused by seasonal factors, the variety of host plants, and genetic factors, coupled with the problem of identifying nymphs to species, contribute to the difficulty in accurately assessing important economic problems.

ORIGIN OF PEST SPECIES

Pest status varies with the organism and resource being evaluated. Acceptable population levels may be low when dealing with disease vectors (Burgess et al., 1983) or much higher when considering certain defoliators. The pest problem then is a relative state dependent on the circumstances. Norton and Conway (1977, p. 205) provided a useful definition: "A pest problem is, therefore, characterized not only by the state of the pest population itself but, more importantly, as the damage or illness it causes and the value placed on these consequences by human society." Several Lygus spp. are considered pests because their feeding damage on certain crops is unacceptable to those involved in crop production (Graham et al., 1984). This damage often is enhanced because lygus bugs frequently feed on reproductive parts of the plant and thus are frequently pests of seed crops (Burgess et al., 1983).

Some Lygus spp. have become pests because they are usually highly mobile, multivoltine, and oligophagous (r-selected), feeding on new growth and reproductive parts. In contrast to many other insect pests in North America, these species are native insects attacking a large array of introduced crops, except in a few instances, such as an Oregon species that feeds on native Limnanthes (meadowfoam) (J.D. Lattin, pers. observ.) and a California species that attacks guayule (Romney, 1946; Bolton et al., 1972; Lattin and Oman, 1983). Price (1976), Southwood (1977), and others have pointed out that many pest herbivores are r-selected species, and in the disturbed environments typical of most agroecosystems, such species can often colonize faster than their predators and parasites. Southwood (1977) stated that polyphagous predators are likely to be important in such habitats. The heteropteran family Nabidae contains several very common, polyphagous predators found frequently in such disturbed habitats in North

---

1/Respectively, Systematic Entomology Laboratory, Agricultural Research Service, U.S. Department of Agriculture, c/o National Museum of Natural History, Washington DC 20560, and Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, OR 97331.

America, for example, Nabis alternatus Parshley and N. americoferus Carayon (Graham and Jackson, 1982).

Lygus bugs, highly mobile as adults, often move from disturbed habitats into crop fields (Fye, 1980). Some species migrate from wild to cultivated plants and have been collected at elevations as high as 5,000 ft (Glick, 1939; Johnson and Southwood, 1949). Although most Lygus spp. are normally multivoltine, single generations may occur in the northern part of their ranges (Kelton, 1975; Craig, 1983). At least one species, Lygus unctuosus (Kelton), may have only a single generation (Kelton, 1975; Craig, 1983). Other univoltine species of Lygus, for example, L. vanduzeei Knight, normally are not economically important (Reid et al., 1976). Care should be taken in determining the actual number of generations (Shull, 1933; Salt, 1945; Craig, 1983).

Feeding occurs most often on growing tips or reproductive parts of the plant, areas of high nutrients. This is particularly damaging to plants grown for seed (Jeppson and MacLeod, 1946; Craig, 1983; Rice et al., 1985). According to Scott (1970, 1983), such feeding might reduce seed yield and germination in carrots, but the plants grown from damaged seed fed on by Lygus spp. may show accelerated growth and larger plants and roots. Conversely, some evidence indicates that such feeding might stimulate increased productivity in some crop species (Scott, 1970). In some instances, the host plant may affect adult longevity and fertility in Lygus bugs (Al-Munshi et al., 1982).

Lygus bugs also feed as scavengers and facultative predators of arthropods. Predation on living insects probably involves moribund individuals or those undergoing ecdysis (Wheeler, 1976). The laboratory rearing of Lygus spp. may be enhanced by adding animal food to the diet (e.g., Bryan et al., 1976).

Several pest species of Lygus are known to occur on a wide variety of plants, both introduced and native (Stitt, 1949; Malcolm, 1953; Parker and Hauschild, 1975; Scott, 1977; Fye, 1980; Snodgrass et al., 1984). Since not all such plant records represent hosts on which eggs are laid, care should be taken to distinguish between hosts, where nymphs occur, and resting or feeding hosts, where only adults are found. Often host plant records in the literature cannot be associated positively with species of Lygus because of the difficulty in making accurate specific identifications and the lack of voucher specimens, particularly in western North America. If voucher specimens have been retained from the numerous economic studies (see Graham et al., 1984), some associations can be verified or corrected. Fortunately the widespread Lygus lineolaris is more easily recognized throughout much of its range than is the complex group of western taxa.

Because legumes frequently are utilized as hosts by North American species of Lygus, it is curious that L. lineolaris, with a large array of hosts (Snodgrass et al., 1984), is not a pest on soybeans, even though this species occurs throughout much of the crop's range and 453 insect species have been recorded from this crop in North America (Kogan, 1981). The establishment and subsequent spread of alfalfa in western North America likely affected significantly the movement and colonization of western species of Lygus bugs (Bolton et al., 1972). The effect of such a crop on the widely scattered, naturally occurring populations of Lygus remains to be studied. When positive species identifications can be combined with accurate host associations, it will be possible to examine the status and distribution of some western Lygus species. This may be an example of "reverse" island biogeography, where a crop plant provides a corridor for dispersal between naturally separated populations.

DEFINITION AND PLACEMENT OF *LYGUS* IN THE FAMILY MIRIDAE

The group of bugs commonly referred to as lygus bugs belongs in the genus Lygus Hahn and to the plant bug family Miridae,

the largest family in the true bug order Heteroptera (superorder Hemiptera). About one-third to one-half of all Heteroptera are mirids. Although fewer than 7,000 species were listed in the Carvalho world Miridae catalog (1957-60), many have been described since the 1950's, probably bringing the total to 10,000 or more. Most mirid workers predict that the species inventory for the world will reach 20,000. Within the Miridae, Lygus is included in the largest subfamily, the Mirinae. According to Carvalho (1957-60), more than 250 mirine genera were described by 1955. Of these, Lygus (sensu lato) contained the greatest number of species, about 300.

Currently, however, only 34 species are placed in Lygus in North America and about 8 are known from the Old World (Kelton, 1975). The reduced number of species recognized in Lygus deserves some explanation. Historically, the broad definition of the Lygus was based largely on the overall similarity of many species, which were inconsistently broken into several similar appearing subgenera. Even so, the economic literature on Lygus was basically stable, and few entomologists were concerned that the pestiferous lygus bugs did not belong in the nominate subgenus Lygus, that is, until more recently, when the type of Lygus became more than an academic problem.

The current classification of Lygus is built primarily on the work of several key workers (appendix). Knight (1917) provided the first comprehensive review of the North American species. He recognized six species groups of Lygus, including his new subgenus Neolygus. China (1941), on discovering that Distant (1904) had designated Cimex pabulinus Linnaeus as the type-species of Lygus, described the subgenus Apolygus (type-species Lygaeus limbatus Fallén) to accommodate what he thought would include Lygus pratensis (L.) and other British "lygus bugs" (China, 1943). Wagner (1949), in a revision of the Palaearctic Lygus, noted that the European L. pratensis was not consubgeneric with species in other subgenera and described the subgenus Exolygus to accommodate it and allies. Leston (1952), in the first attempt to evaluate internal relationships of the genus on a worldwide basis, recognized six subgenera, including his new subgenus Taylorilygus, which contained Lygus pallidulus (Blanchard) (as Lygus apicalis Fieber, a junior synonym) and the African "lygus bugs."

Leston's work served as the basis for an important revision by Kelton (1955a), who, by utilizing male and female genitalia and external morphology, gave strong evidence that most of the subgenera previously placed in Lygus deserved generic status. He recognized as valid genera Agnocoris Reuter (type-species Lygaeus rubicundus Fallén), Liocoris Fieber (type-species Cimex tripustulatus Fabricius) (with Exolygus Wagner as a junior synonym (type-species Cimex pratensis Linnaeus)), Lygus Hahn (type-species Cimex pabulinus Linnaeus), Orthops Fieber (type-species Cimex kalmii Linnaeus), and Taylorilygus Leston (type-species Lygus simonyi Reuter) (appendix). This revision produced the result Slater (1950) had predicted should several subgenera in Lygus be raised to genus, viz, that the economically important lygus bugs would be placed in a genus other than Lygus. Because the North American lygus bugs are congeneric with Cimex pratensis (the type-species of Exolygus), Kelton's revision required that they be transferred to Exolygus. Kelton (1955a, 1955b) considered Exolygus a junior synonym of Liocoris, meaning, that if this interpretation was followed, the lygus bugs would take the generic name Liocoris. Wagner (1957), however, maintained that Exolygus and Liocoris were not congeneric, leaving the status of Exolygus problematic.

To prevent such an upheaval in the economic literature, Carvalho, Knight, and Usinger (1961), with the agreement of most of the mirid-worker community, including Kelton, petitioned the International Commission of Zoological Nomenclature (I.C.Z.N.) to reject Cimex pabulinus as the type of the subgenus

Lygus and to designate Cimex pratensis as the type-species. The I.C.Z.N. (Opinion 667, 1963) thus ruled to preserve the well-known concept of Lygus with the following decisions:

(1) Lygus Hahn, 1833 (fix Cimex pratensis Linneaus, 1758, as the type-species).
Exolygus Wagner, 1949 (type-species Cimex pratensis Linneaus), an objective junior synonym of Lygus to be placed on the list of officially rejected names.

(2) Lygocoris Reuter, 1875 (fix Cimex pabulinus Linneaus, 1761, as the type-species).

These changes have insured that the economic lygus bugs will remain in the genus Lygus and that Exolygus will always be a junior synonym because they have the same type-species. Presently, Liocoris is considered distinct from Lygus, but if Kelton's conclusions are followed, it becomes a junior synonym of Lygus.

GENERIC AND SPECIES RECOGNITION

Nearctic Taxa

Anyone who has tried to identify species of Lygus will agree that the genus is particularly difficult to define. Carvalho (1955) in a monumental effort probably illustrates it best. Of 154 mirine genera in his "Keys to the Genera of the Miridae of the World," Lygus falls out at couplet 153, a clear indication that the genus is most easily diagnosed by eliminating the other more "distinct" genera. Carvalho's study, however, predated Kelton (1955a) and others who published their interpretations of the Lygus complex. Kelton's (1955a) key to genera of the Lygus complex, if used in conjunction with the more comprehensive keys of Blatchley (1926), Knight (1941, 1968), and Kelton (1980) to reach the Lygus complex, will allow relatively easy recognition of the North American genera. Slater and Baranowski's (1978) publication contains the only recent key to genera of North American Miridae. Its simple terminology with numerous illustrations makes it a good generic reference.

At the species level, Kelton's (1975) revision of North American Lygus is the best reference to consult. It contains a key and descriptions of all recognized species, notes on their distribution and hosts, and clarification of earlier misidentifications of Palaearctic species. Although he reevaluated the Nearctic fauna and recognized several synonyms, determination of species remains difficult, even for the specialist with correctly identified specimens for comparison. Most species of Lygus are multivoltine and have numerous seasonal or color forms, which compound the degree of difficulty in species recognition. In table 1 is a summary of overwintering stages, voltinism, and host plant groups of Lygus and associated genera. Current difficulties in associating certain populations of Lygus with specific names indicate that some of the 34 Nearctic species may be conspecific.

Palaearctic Taxa

For the Palaearctic region, several good references can be used to identify genera and species. Southwood and Leston (1959) provided a key to the species and genera of the tribe Mirini found in the British Isles. Stichel's (1958) publication is one of the best for the European species of Miridae. Kiritshenko's (1951) keys to the bugs of the European U.S.S.R., although having an outdated generic scheme, can be used for species identifications. Kerzhner's (1964) key is good for the genera and the species found in the European U.S.S.R.; Vinokurov's (1979) key is available for the more eastern region of Yakut. Wagner's (1970-71) key to the Miridae of the Mediterranean region, although still using the name Exolygus instead of Lygus, is the most recent and comprehensive European reference. As in North America, the species are variable and often difficult to recognize with certainty.

Table 1
General life history and host information of *Lygus* and other genera previously included in the *Lygus* complex

Genus	Overwintering stage	Number of generations	Hosts
Agnocoris	Adult	Multiple (?)	Host specific on *Salix* spp.
Dagbertus	Adult and egg (?)	Multiple	Polyphagous
Lygocoris			
Subg. *Apolygus*	Egg	Single	Polyphagous (?) weeds and trees
Subg. *Lygocoris*	Egg	Multiple	Polyphagous
Subg. *Neolygus*	Egg	Single	Host specific on trees and shrubs
Lygus [1/]	Adult	Multiple	Polyphagous
	Egg	Single	Host specific
Orthops	Adult	Multiple (?)	Host specific on Umbelliferae
Pinalitus	Egg	Single	Host specific on *Picea* and *Pinus* spp.
Taylorilygus	Adult and egg	Multiple	Polyphagous

[1/] Appears to have 2 distinct species groups.

IDENTIFICATION OF NYMPHS

Late-instar nymphs of North American Miridae may be recognized using several nymphal keys, including DeCoursey (1971), Herring and Ashlock (1971), and Slater and Baranowski (1978). Southwood (1956) developed a key for determining the instar of cimicomorphan nymphs. Leston and Scudder (1956) gave descriptions and family keys to the nymphs of the British Heteroptera. Butler's (1923) "Biology of the British Hemiptera-Heteroptera" contains descriptions, life histories, and hosts of many species, including those in the *Lygus* complex found in the British Isles. Bech (1969) should be consulted for information on the life history, ecology, and nymphs and particularly for the long host list of the Palaearctic species of *Lygus* and related genera. In both of the last texts, an older scheme of classification, similar to that presented by Wagner (1949), is given. Users of these references need to update the generic placement of the species treated.

Akingbohungbe et al. (1973) published the only text containing nymphal keys to the genera of Miridae in North America. Their "Keys to the Nymphs of the Wisconsin Miridae" show that it is possible to recognize genera and even species of Miridae in the immature stages.

RELATIONSHIPS OF GENERA PREVIOUSLY PLACED IN *LYGUS*

Agnocoris Reuter. The Holarctic willow-feeding genus *Agnocoris* externally is similar to *Lygus*, but the genital structures, silky pubescence, and short second antennal segment define a

distinct genus (Kelton, 1955a). Although Slater (1950) believed the female genitalia of Agnocoris were rather distinct from those of other Lygus groups (subgenera), Kelton (1955a) suggested that Agnocoris, along with the Palaearctic genus Cyphodema Fieber, was one of the few genera previously placed in the Lygus complex that showed close relationship to Lygus.

Knightomiris Kelton. The parameres of Knightomiris distinctus (Knight) are similar to those of Lygus, but K. distinctus has a prominent tubercle on the margin of the pygophore above the left paramere and the vesica differs in having two distinct spiculi (Kelton, 1974). Kelton erected Knightomiris to accommodate this single species.

Lygocoris Reuter. This genus, now divided into four subgenera, probably has little relationship to Lygus. Slater (1950) indicated that the subgenus Neolygus does not appear even closely related to Lygus. Kelton (1955a) confirmed that male and female genitalia and many external characters linked the subgenera Apolygus, Lygocoris, Neolygus, and Stechus. Based on this information, Kelton considered Lygocoris distinct from Lygus [as Liocoris]. Clayton (1982) further supported the distinctiveness of Lygocoris and suggested that the subgenera Apolygus, Lygocoris, and Neolygus might best be considered as separate genera. Zheng and Wang (1982, 1983) and Wang and Zheng (1982), although apparently correctly placing 20 new species from China in Apolygus, incorrectly placed them in the genus Lygus. As members of the subgenus Apolygus, they must be placed in the genus Lygocoris. Kelton (1971) reviewed the Nearctic species of Lygocoris, redescribed the adults, furnished host plant information, and provided a key to help distinguish species found in Canada and Alaska.

Orthops Fieber. Wagner's (1949) vague definition of Orthops includes a group of heterogeneous species (Kelton, 1955a). Kelton's study of the Palaearctic species visicola (Puton), cervinus (Herrich-Schaeffer), atomarius (Meyer-Dür), and rubricatus (Fallén) indicated that they were not congeneric with kalmii Linnaeus, the type-species of Orthops. Later, the spruce-feeding rubricatus was transferred to Pinalitus Kelton with the pine-feeding approximatus Stål (Kelton, 1977) and three other Nearctic species. Kelton (1955a) considered the umbelliferous-feeding species of the genus Orthops remotely related to Lygus. Orthops is considered closely related to the Afro-tropical genus Lygidolon Reuter, which has been reviewed by Odhiambo (1960), Ghauri (1971), and Linnavuori (1974). Linnavuori (1975) noted that the African species of Lygidolon, Orthops, and Taylorilygus need to be revised and should be studied along with the genera Gutrida Kirkaldy, Oreolygus Linnavuori, and Yngveella Poppius.

Pinalitus Kelton. The genus Pinalitus, erected to accommodate the species approximatus Stål, apparently is related to the Neotropical genus Alda, but it differs in having a much shorter first antennal segment (Kelton, 1955a). Alda resembles certain members of the widely distributed genus Phytocoris Fallén and, like Pinalitus, is not closely related to Lygus.

Proba Distant. The species Lygus sallei Stål, included in Knight's (1917) catchall group I, now is placed in the Neotropical genus Proba. Carvalho (1952) previously considered Paralygus Reuter a junior synonym of Proba.

Kelton (1955a) noted a superficial resemblance of Proba to Horcias Distant (the latter is now in part subdivided, with the North American species transferred to the genus Metriorrhynchomiris Distant (Carvalho and Jurberg, 1974)), but he stated that the absence of a transverse carina between the eyes and the form of the genital structures on Horcias easily separated it from Proba.

Sabactus Distant. Another monotypic genus known from Sri Lanka, it contains only the species institutus (Distant).

Previously this genus was placed in Lygus, but Kelton showed that the two genera are not closely related.

Salignus Kelton. This Nearctic, monotypic genus (Kelton, 1955a) possesses unique characters making it distinct from Lygus. Salignus distinguendus (Knight), a willow-feeding species, differs in structure from any taxon studied by Kelton (1955a).

Taylorilygus Leston. Kelton (1955a) considered Leston's subgenus Taylorilygus a distinct genus, noting that the male and female genitalia indicated it was not closely related to Lygus. All species of Taylorilygus are confined to the Afro-tropical region, except T. pallidulus (Blanchard), a polyphagous "cosmopolitan" species. Taylor (1947) described most of the species, indicated host plants, and provided an identification key. Kelton (1955a) considered Taylorilygus most closely related to the Neotropical genus Dagbertus Distant. These two genera are similar externally, but the genital structures and the very short third antennal segment of Dagbertus will distinguish them (Kelton, 1955a; Slater and Baranowski, 1978). Carvalho (1983) reviewed Dagbertus, providing descriptions of 12 new species, a checklist of the species, and a key to help separate them.

PROBLEMS INVOLVING THE TAXONOMY OF NORTH AMERICAN *LYGUS*

Despite efforts to clarify the species level taxonomy of Lygus and related genera, it is difficult to positively identify many commonly encountered specimens. This hinders the development of species-specific programs involving, for example, biological control agents. The taxonomic difficulty stems chiefly from the inability to determine species in Lygus accurately and from their variability throughout their ranges. Macromorphological systematic techniques may have been used to their limit. Micromorphological studies, including the use of the scanning electron microscope (SEM), are called for and, in fact, have produced some promising results on a limited basis (J.D. Lattin and V. Razafimahatratra, unpub.).

Contemporary biochemical techniques should be used, such as those of Sluss et al. (1982), together with crossbreeding investigations (Graham, 1982). The development of an artificial diet for Lygus makes easier the maintenance of laboratory cultures for study (Debolt, 1982). Sex pheromones have been detected in several species of Miridae, including Lygus, and should be investigated further (Boivin and Stewart, 1982). Adequate samples, well documented and appropriately preserved, should be collected over a wide area. Such samples would also assist in studies involving geographic variation. Because considerable seasonal variation in the adults is known to occur (Kelton, 1975), samples should be taken during more than one season.

It is not now possible to identify nymphs to species accurately. Well-preserved nymphs associated with adults should be collected for study. Some mirid nymphs can be identified to species in other genera, but comparatively little work has been done on nymphal taxonomy (see previous section on nymphs). It also is possible that useful taxonomic characters might be found on the eggs of Lygus. The SEM would be an essential investigative tool for such work. All the available information should be assembled and analyzed utilizing contemporary systematic methods.

Once a more solid systematic base has been established, it may be possible to clarify other puzzling questions, for example, the broad geographical ranges of many species that often overlap those of several others. Is this the case, or are we unable to recognize other taxa adequately, or are they the same species? It is clear that there is seasonal variation and, most likely, geographical variation. We are not yet able to cope fully with these

variables. Carefully conducted life history studies, with voucher specimens, are needed to clarify these problems.

The available host plant data present a bewildering array of plant taxa with few indications of any ordered associations. Clear distinction should be made between resting, feeding, and hosts supporting nymphs such as was done by Fye (1980) or Snodgrass et al. (1984), who indicate when adults or nymphs or both were collected. Damage can occur on crops where Lygus bugs do not breed and oviposit, especially because adults readily migrate to and feed on plants where nymphs do not occur.

Careful attention should be given to the phenology of the host plant and the occurrence of Lygus on the plant. Almost certainly some of the apparent confusion over host association is due to host plant shifts in different parts of the bug's range. Fox and Morrow (1981) pointed out that a species may be a generalist throughout its range but a specialist locally. Species of the genus Lygus would seem to be excellent subjects for such an analysis once the taxonomy is better known. A species such as Lygus lineolaris, already well defined but very widespread and apparently rather polyphagous, would be a fine candidate for such a study.

And finally, if a rational approach is to be taken in seeking possible biological control agents, particularly in other parts of the world, it is essential to know just where the genus Lygus fits in the overall phylogeny of the Miridae. A more indepth comparison of the mirine genera is needed using contemporary phylogenetic analysis. When we know more about the near relatives of Lygus and where they occur, searches for more effective biological control agents are likely to be more successful. Although there is no guarantee that seeking such agents from near relatives will produce successful results, it does put such efforts on a more ordered basis (Condit and Cate, 1982).

RECOMMENDATIONS FOR FUTURE WORK

(A) Short term
- (1) Adults
  - Micromorphological studies
  - Biochemical studies, including allozymes and pheromones
  - Hybridization studies
  - Adequately vouchered and preserved samples from broad geographical areas
- (2) Nymphs and eggs
  - Procurement of associated samples
  - Micromorphological studies
- (3) General
  - Accurate, vouchered host data over broad geographical area
  - Thorough life history studies, including hosts, phenology, and population dynamics
  - Studies of associated predators and parasites

(B) Long term
- Analysis and synthesis of short-term information
- Systematic revision of the genus Lygus
- Phylogenetic studies of Lygus spp. and near relatives
- Host plant resistance studies

SOME FINAL QUESTIONS

A review of this kind frequently raises more questions than it answers. Our knowledge is so rudimentary in some areas as to make progress difficult. Nevertheless, some intriguing questions may be raised, the answers to some of which may eventually come from work on Lygus.

- --What makes the native species of Lygus move so readily to introduced plants, including crop plants?
- --Although some Lygus feed on various legumes, why have they not transferred to soybeans, even though a large number of other insects have done so, including Lygocoris (Apolygus) lucorum (Meyer-Dür) (Lattin and Hall, 1983)?
- --How is it possible to explain the apparent great range of acceptable

host plants for some Lygus species? There are species included in the genus that appear to be host-plant specific and may be typical k-selected species.

--What adaptive features of Lygus spp. enable them to occupy (apparently) such a wide geographic range? Can these attributes be identified and included in predictive models on pest potential?

--Some species of Lygus are sometimes found together on crops. What are the consequences of this apparent interspecific competition?

--Are there special attributes of the pest species of Lygus that allow them to adjust to unstable, disturbed environments and thereby enable them to become pests in the first place? Are they less of a problem in no-tillage systems?

--What can be learned by analyzing the nature of the predator-parasite complex associated with each species of Lygus, including those that are not pests?

--Why haven't some Lygus species been introduced into other countries accidentally?

--Although many European insects have been introduced into North America, including a large number of Miridae, where are the common European species of Lygus? Several European species of Lygus are regularly intercepted at U.S. ports by APHIS Plant Pest Quarantine personnel (pers. observ., T.J. Henry). All earlier reports of European species of Lygus in North America apparently are based on misidentifications. It is possible that some of these species are present in our fauna but have gone undetected. If not, why haven't these species become established?

Quite clearly, although much is known about Lygus bugs and many authors have contributed to this knowledge, there is much to learn.

ACKNOWLEDGMENTS

We thank V.D. Razafimahatratra, National University, Malagasy Republic, Madagascar, for sharing his views on some of the problems in the genus Lygus. Many useful suggestions have been made by R.C. Froeschner, Department of Entomology, National Museum of Natural History (NMNH), Washington, D.C.; R.W. Hodges, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o NMNH; and A.G. Wheeler, Jr., Bureau of Plant Industry, Pennsylvania Department of Agriculture, Harrisburg, Pa.

REFERENCES CITED

Akingbohungbe, A.E., J.L. Libby, and R.D. Shenefelt. 1973. Nymphs of Wisconsin Miridae. Hemiptera: Heteroptera. Univ. Wis. Expt. Sta. Bul. R2561, 24 pp.

Al-Munshi, D.M., D.R. Scott, and H.W. Smith. 1982. Some plant host effects on Lygus hesperus (Hemiptera: Miridae). Jour. Econ. Entomol. 75:813-815.

Bech, R. 1969. Untersuchungen zur Systematik. Biologie und Ökologie wirtschaftlich wichtiger Lygus-Arten. (Hemiptera: Miridae). Beitr. Ent. 19:63-103.

Blatchley, W.S. 1926. Heteroptera or true bugs of eastern North America. 1116 pp. Nature Pub. Co., Indianapolis, Ind.

Boivin, G., and R.K. Stewart. 1982. Attraction of male green apple bugs, Lygocoris communis (Hemiptera: Miridae), to caged females. Can. Entomol. 114:765-766.

Bolton, J.L., B.P. Goplen, and H. Baenziger. 1972. World distribution and historical developments. In Hanson, C.H., ed., Alfalfa Science and Technology, pp. 1-34. Amer. Soc. Agron., Inc., Madison, Wis.

Bryan, D.E., C.G. Jackson, R.L. Carranza, and E.G. Neeman. 1976. Lygus hesperus: Production and development in the laboratory. Jour. Econ. Entomol. 69:127-129.

Burgess, L., J. Dueck, and D.L. McKenzie. 1983. Insect vectors of the yeast Nematospora coryli in mustard, Brassica juncea, crops in southern Saskatchewan. Can. Entomol. 115:25-30.

Butler, E.A. 1923. A biology of the British Hemiptera-Heteroptera. 682 pp. H.F. & G. Witherby, London.

Carvalho, J.C.M. 1952. On the major classification of the Miridae (Hemiptera). (With keys to subfamilies and tribes and a catalogue of the world genera.) Acad. Brasil. Cien. 25:31-110.

Carvalho, J.C.M. 1955. Keys to the genera of Miridae of the world (Hemiptera). Bol. Mus. Goeldi. 11:1-151.

Carvalho, J.C.M. 1957-60. Catalog of the Miridae of the world. Pt. I (44(1):1-158 (1957)), pt. II (45(2):1-216 (1958)), pt. III (47(3):1-161 (1958)), pt. IV (48(4):1-384 (1959)), pt. V (51(5):1-194 (1960)). Arq. Mus. Nac., Rio de Janeiro 48:1-384.

Carvalho, J.C.M. 1983. Mirideos neotropicais CCXXXIII: Gênero Dagbertus Distant--Descriçoes de espécies e revisao das que ocorrem na regiao (Hemiptera). Rev. Brasil. Biol. 43:157-176.

Carvalho, J.C.M., and J. Jurberg. 1974. Neotropical Miridae, CLXXX: On the Horcias complex (Hemiptera). Rev. Brasil. Biol. 34:49-65.

Carvalho, J.C.M., H.H. Knight, and R.L. Usinger. 1961. Lygus Hahn, 1833 (Insecta, Hemiptera); proposed designation under the plenary powers of the type-species in harmony with accustomed usage. ZH.(S.) 1062. Bul. Zool. Nomencl. 18:281-284.

China, W.E. 1941. A new subgeneric name for Lygus Reuter 1875 nec Hahn 1833 (Hemipt.-Heteropt.). Proc. Roy. Entomol. Soc. Lond. 10:60.

China, W.E. 1943. The generic names of British Hemiptera-Heteroptera, with a check list of the British species. 316 pp. Roy. Entomol. Soc. Lond.

Clayton, R.A. 1982. A phylogenetic analysis of Lygocoris Reuter (Heteroptera: Miridae) with notes on life histories and zoogeography. M.S. Thesis, Univ. Conn., Storrs, 78 pp.

Condit, B.P., and J.R. Cate. 1982. Determination of host range in relation to systematics for Peristenus stygicus (Hym.: Braconidae), a parasite of Miridae. Entomophaga 27:203-210.

Craig, C.H. 1983. Seasonal occurrence of Lygus spp. (Heteroptera: Miridae) on alfalfa in Saskatchewan. Can. Entomol. 115:329-331.

Debolt, J.W. 1982. Meridic diet for rearing successive generations of Lygus hesperus. Ann. Entomol. Soc. Amer. 75:119-122.

DeCoursey, R.M. 1971. Keys to the families and subfamilies of the nymphs of North American Hemiptera-Heteroptera. Proc. Entomol. Soc. Wash. 73:413-428.

Distant, W.L. 1904. The fauna of British India including Ceylon and Burma. Rhynchota. Vol. II. (Heteroptera). 503 pp. Taylor and Francis Printers, London.

Fox, L.R., and P.A. Morrow. 1981. Specialization: Species property or local phenomenon? Science 211:887-893.

Fye, R.E. 1980. Weed sources of Lygus bugs in the Yakima Valley and Columbia Basin in Washington. Jour. Econ. Entomol. 73:469-473.

Ghauri, M.S.K. 1971. New species of Lygidolon Reuter (Hemiptera-Heteroptera: Miridae) infesting wattle in South and East Africa. Jour. Entomol. 40:133-138.

Glick, P.A. 1939. The distribution of insects, spiders and mites in the air. U.S. Dept. Agr. Tech. Bul. 673:1-150.

Graham, H.M. 1982. Interbreeding of Lygus elisus Van Duzee and L. desertinus Knight in the field. Southwest. Entomol. 7:60-64.

Graham, H.M., and C.G. Jackson. 1982. Distribution of eggs and parasites of Lygus spp. (Hemiptera: Miridae), Nabis spp. (Hemiptera: Nabidae), and Spissistilus festinus (Say) (Homoptera: Membracidae) on plant stems. Ann. Entomol. Soc. Amer. 75:56-60.

Graham, H.M., A.A. Negm, and L.R. Ertle. 1984. Worldwide literature of the Lygus complex (Hemiptera: Miridae), 1900-1980. U.S. Dept. Agr., Agr. Res. Serv., Bibliogr. Lit. Agr. No. 30, 205 pp.

Herring, J.L., and P.D. Ashlock. 1971. A key to the nymphs of the families of Hemiptera (Heteroptera) of America north of Mexico. Fla. Entomol. 54:207-212.

International Commission of Zoological Nomenclature. 1963. Opinion 667. Bul. Zool. Nomencl. 20:270-271.

Jeppson, L.R., and G.F. MacLeod. 1946. Lygus bug injury and its effect on the growth of alfalfa. Hilgardia. 17:165-188.

Johnson, C.G., and T.R.E. Southwood. 1949. Seasonal records in 1947 and 1948 of flying Hemiptera-Heteroptera, particularly Lygus pratensis L., caught in nets 50 ft to 3,000 ft above ground. Proc. Roy. Entomol. Soc. Lond. (A) 24:128-130.

Kelton, L.A. 1955a. Genera and subgenera of the Lygus complex (Hemiptera: Miridae). Can. Entomol. 87:277-301.

Kelton, L.A. 1955b. Species of Lygus, Liocoris, and their allies in the Prairie Provinces of Canada. Can. Entomol. 87:531-556.

Kelton, L.A. 1971. Review of Lygocoris species found in Canada and Alaska (Heteroptera: Miridae). Entomol. Soc. Canada Mem. 83:1-87.

Kelton, L.A. 1974. Knightomiris new genus, for Lygus distinctus (Heteroptera: Miridae). Can. Entomol. 105:1417-1420.

Kelton, L.A. 1975. The lygus bugs (genus Lygus Hahn) of North America (Heteroptera: Miridae). Entomol. Soc. Canada Mem. 95:1-101.

Kelton, L.A. 1977. Species of the genus Pinalitus Kelton found in North America (Heteroptera: Miridae). Can. Entomol. 109:1549-1554.

Kelton, L.A. 1980. The plant bugs of the Prairie Provinces. Heteroptera: Miridae. Agr. Can. Pub. 1703, 408 pp. Ottawa.

Kerzhner, I.M. 1964. Order Hemiptera (Heteroptera). Family Miridae (Capsidae). In Bei-Bienko, G.Y., ed., Keys to the Insects of the European U.S.S.R., vol. I, pp. 911-1003, Apterygota, Paleoptera, Hemimetabola. Zool. Inst. Acad. Sci. U.S.S.R., Leningrad. [English transl., 1967; Russian edition, 1964]

Kiritshenko, A.N. 1951. True bugs of the European U.S.S.R. (Hemiptera). Key and bibliography. 423 pp. Acad. Sci. U.S.S.R., Moscow-Leningrad. [In Russian]

Knight, H.H. 1917. A revision of the genus Lygus as it occurs in America north of Mexico, with biological data on the species from New York. Cornell Univ. Agr. Expt. Sta. Bul. 391:555-645.

Knight, H.H. 1941. The plant bugs, or Miridae, of Illinois. Ill. Nat. Hist. Surv. Bul. 22:1-234.

Knight, H.H. 1968. Taxonomic review: Miridae of the Nevada Test Site and the Western United States. Brigham Young Univ. Sci. Bul. 9(3):1-282.

Kogan, M. 1981. Dynamics of insect adaptations to soybeans: Impact of integrated pest management. Environ. Entomol. 10:363-371.

Lattin, J.D., and B.B. Hall. 1983. Lygocoris (Apolygus) lucorum (Meyer-Dür) 1843 (Hemiptera: Miridae). Potential host of parasites for biological control of Lygus. Oreg. State Univ., Syst. Entomol. Lab. Inform. Sheet, 2 pp.

Sluss, T.P., H.M. Graham, and E.S. Sluss. 1982. Morphometric, allozyme, and hybridization comparisons of four Lygus species (Hemiptera: Miridae). Ann. Entomol. Soc. Amer. 75:448-456.

Snodgrass, G.L., W.P. Scott, and J.W. Smith. 1984. An annotated list of the host plants of Lygus lineolaris (Hemiptera: Miridae) in the Arkansas, Louisiana, and Mississippi Delta. Jour. Ga. Entomol. Soc. 19:93-101.

Southwood, T.R.E. 1956. A key to determine the instar of an heteropterous larva. Entomologist 89:220-222.

Southwood, T.R.E. 1977. The relevance of population dynamic theory to pest status. In Cherrett, J.M., and G.R. Sagar, eds., Origins of Pest, Parasite, Disease and Weed Problems, pp. 35-54. 18th Symp. Brit. Ecol. Soc., Bangor, 12-14 Apr. 1976. Blackwell Sci. Pub., Oxford.

Southwood, T.R.E., and D. Leston. 1959. Land and water bugs of the British Isles. 436 pp. Frederick Warne & Co. Ltd., London.

Stichel, W. 1958. Illustrierte Bestimmungstbellen der Wanzen. II. Europa (Hemiptera-Heteroptera Europae). Vol. 2, 24 Heft, pp. 737-768. Martin-Luther, Berlin-Hermsdorf.

Stitt, L.L. 1949. Host-plant sources of Lygus spp. infesting the alfalfa seed crop in southern Arizona and southeastern California. Jour. Econ. Entomol. 42:93-99.

Taylor, T.J.C. 1947. Some East African species of Lygus, with notes on their host plants. Bul. Entomol. Res. 38:233-258.

Vinokurov, N.N. 1979. Keys to the fauna of the U.S.S.R. Heteropterous insects of Yakutia. 231 pp. Zool. Inst., Acad. Sci. U.S.S.R., Leningrad. [In Russian]

Wagner, E. 1949. Zur Systematik der Gattung Lygus Hhn. (Hem. Het. Miridae). Verh. Ver. Naturw. Heimatf., Hamburg. 30:26-40.

Wagner, E. 1957. Das Lygus-Liocoris Problem (Hem. Het. Miridae). Deut. Entomol. Ztschr. 4:91-94.

Wagner, E. 1970-71. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makaronesischen Inseln (Hemiptera, Heteroptera). Teil 1. Entomol. Abh. Mus. Tierk. Dresden, Sup. 37:1-484. [1970:1-273; 1971:274-484]

Wang, X., and L. Zheng. 1982. Three new species of Lygus of the subgenus Apolygus from Fujian, China (Hemiptera: Miridae). Wuyi Sci. Jour. 2:118-123.

Wheeler, A.G., Jr. 1976. Lygus bugs as facultative predators. In Scott, D.R., and L.E. O'Keeffe, eds., Lygus Bugs: Host Plant Interactions, pp. 28-35. Univ. Idaho Press, Moscow.

Zheng, L., and X. Wang. 1982. New species of Lygus bugs from China. Entomotaxonomia 5:47-59.

Zheng, L., and X. Wang. 1983. New species and records of Lygus (subg. Apolygus) from China. Acta Zootaxonom. Sinica. 8:422-433.

APPENDIX

The following classifications of *Lygus* are from Knight (1917) to the present:

(1) Knight (1917) treated only North American taxa:
- Genus *Lygus* Hahn
  - Group I (*pratensis* group; considered *Lygus lineolaris* (Palisot) a junior synonym of *Lygus pratensis* (Linneaus))
  - Group II (*campestris* group)
    - *campestris* Linneaus (subg. *Orthops* Fieber)
    - *distinctus* Knight (now in *Knightomiris* Kelton)
    - *rubicundus* Fallén (subg. *Agnocoris* Reuter)
    - *sallei* Stål (now in *Proba* Distant)
  - Group III *approximatus* Stål (now in *Pinalitus* Kelton)
  - Group IV
    - *fasciatus* Reuter (now in *Dagbertus* Distant)
    - *olivaceus* Reuter (now in *Dagbertus*)
  - Group V
    - *apicalis* Fieber (now in *Taylorilygus* Leston)
  - Group VI (*communis* group; subg. *Neolygus* Knight) contains 39 species in North America

(2) China (1943) treated British genera:
- Genus *Liocoris* Fieber (type-species *tripustulatus* (Fabricius))
- Genus *Lygus*
  - Subgenus *Agnocoris* (type-species *rubicundus*)
  - Subgenus *Apolygus* China (type-species *limbatus* Fallén)
  - Subgenus *Lygus* (type-species *pabulinus* Linnaeus)
  - Subgenus *Orthops* (type-species *kalmii* Linnaeus)

(3) Wagner (1949) treated Palaearctic genera:
- Genus *Lygus*
  - Subgenus *Agnocoris* (type-species *rubicundus*)
  - Subgenus *Apolygus* (type-species *limbatus*)
  - Subgenus *Exolygus* Wagner (type-species *pratensis*)
  - Subgenus *Lygus* (type-species *pabulinus*)
  - Subgenus *Orthops* (type-species *kalmii*)

(4) Leston (1952) gave a world review of *Lygus* and subgenera:
- Genus *Lygus*
  - Subgenus *Agnocoris* (type-species *rubicundus*)
  - Subgenus *Exolygus* (type-species *pratensis*)
  - Subgenus *Lygus* (type-species *pabulinus*)
  - Subgenus *Neolygus* (type-species *communis* Knight)
  - Subgenus *Apolygus*, a junior synonym (type-species *limbatus*)
  - Subgenus *Orthops* (type-species *kalmii*)
  - Subgenus *Taylorilygus* Leston (type-species *simonyi* Reuter)

(5) Kelton (1955a) treated *Lygus* and associated genera:
- Genus *Agnocoris* (type-species *rubicundus*)
- Genus *Cyphodema* Fieber (type-species *instabilis* Lucas)
- Genus *Dagbertus* (type-species *darwini* Butler)
- Genus *Liocoris* (type-species *tripustulatus*)
- Genus *Exolygus*, a junior synonym (type-species *pratensis*)
- Genus *Lygus* (type-species *pabulinus*)
  - Subgenus *Apolygus* (type-species *limbatus*)
  - Subgenus *Lygus* (type-species *pabulinus*)
  - Subgenus *Neolygus* (type-species *communis*)
  - Subgenus *Stechus* Distant (type-species *libertus* Distant)
- Genus *Orthops* Fieber (type-species *kalmii*)
- Genus *Pinalitus* (type-species *approximatus*) (group III of Knight (1917))
- Genus *Proba*

(type-species gracilis Distant)
(sallei group of Knight (1917))
Genus Sabactus Distant
(type-species institutus Distant)
Genus Salignus
(type-species distinguendus Reuter)
(in group I of Knight (1917))
Genus Taylorilygus
(type-species simonyi)

(6) Current scheme, ruling of International Commission of Zoological Nomenclature (1963); other generic concepts (not listed) follow Kelton (1955a, 1974):
Genus Liocoris
(a subjective junior synonym of Lygus; currently considered a distinct genus)
Genus Lygocoris
(type-species pabulinus)
Subgenus Apolygus
(type-species limbatus)
Subgenus Lygocoris
(type-species pabulinus)
Subgenus Neolygus
(type-species communis)
Subgenus Stechus
(type-species libertus)
Genus Lygus
(type-species pratensis)
Genus Exolygus (same type-species; an objective junior synonym of Lygus)