INTRODUCTION TO
ATTACK AND DEFENSE: BEHAVIORAL ECOLOGY OF PARASITES AND PARASITOIDS AND THEIR HOSTS.

BEHAVIORAL ECOLOGY: FROM FABULOUS PAST TO CHAOTIC FUTURE

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Genesis of this symposium on behavioral ecology owes something to Sir Francis Drake. His observations in 1579 in the Moluccas were recorded by Hakluyt (ca. 1588) in the following terms. “Amongst these trees night by night, through the whole land, did shew themselves an infinite swarm of fiery wormes flying in the ayre, whose bodies beeing no bigger then our common English flies, make such a shew and light, as if every twigge or tree had bene a burning candle.”

The spectacular nature of flashing by fireflies in countries of the southwestern Pacific basin attracted the curiosity of James Lloyd (Lloyd 1973). Lloyd’s discoveries on fireflies were observational and interpretive and, when he discovered the existence of behavioral ecology as a discipline, he knew he had found his niche (Lloyd 1980). The first seven symposia held by this society and organized by James Lloyd explored the panoply of behavioral ecology and fascinated the audiences. The eighth symposium, organized by Earl McCoy and Don Strong, introduced a theme to the event, and the theme then was of their choosing: The Behavioral Ecology of Colonization.

This ninth symposium also has a theme: Attack and Defense - The Behavioral Ecology of Parasites and Parasitoids and their Hosts. The theme was chosen on the premise that biological control is a rising area of research, and that much that is novel and interesting in behavioral ecology is being done under the auspices of biological control. Evolution of words in the field of ecology and its subdiscipline biological control prompts us here to attempt an etymological clarification.

The noun parasite has been used in English for many hundreds of years, and the noun parasitism at least since the early 17th century (OED 1971). It was unnecessary therefore to derive the noun parasitization (as a synonym of parasitism) from the verb to parasitize. The word parasitization is also longer and clumsier and smacks of the excesses of Orwell’s newspeak (Orwell 1949).

The nouns parasite and predator were used until the 20th century to describe animals which feed on other animals, but then two inadequacies were raised. One inadequacy was in the definition of the behavior of parasites. If we take the definition of parasite to include only those animals which do not kill their hosts in the sense of having achieved an evolutionary balance between the immediate and long-term nutritional needs of the parasite, as exemplified in Aesop’s fable The Goose with the Golden Eggs (Fig. 1), then another word is required for parasite-like animals which do kill their
hosts. This word, parasitoid, was supplied by Reuter (1913), and has been adopted into English (OED 1971). Yet, in much entomological writing, the word parasite is used in the older sense to include parasitoid as well as parasite (in the strict sense). Perhaps this failure to use the word parasitoid wherever it applies is because of uncertainty of the status of the corresponding noun parasitoidism, verb to parasitoidize, adverb parasitoidally, and adjective parasitoidal. However, logic directs that these words be used wherever they are needed.

With acceptance of the noun parasitoid, the three definitions are as follows. Parasite: An organism that lives in or on the body of its host without killing the host, but usually debilitating the host to some extent. Parasitoid: An organism that, during its development, lives in or on the body of a single host individual, eventually killing that individual. Predator: An organism that, during its development, consumes more than one prey individual.

The other inadequacy was in the concept of the sort of host or prey consumed. A popular English name for aphid is plant-louse, implying that aphids, just as lice, are parasites. The definition above of parasite specifies the body of its host, and body is defined by Webster (1986) as the organized physical substance of an animal or plant either living or dead. Therefore, the definitions above do allow inclusion of plants as hosts of parasites and parasitoids and as prey of predators. To make certain of this inclusion in the literature of ecology, Price (1975) wrote of aphids, weevils, etc. as parasites of plants, while Janzén (1971, 1975) wrote of beetles as predators and parasitoids of seeds and coined the expression seed-predator. Grazing by cattle on plants could be considered as parasitism if we disregard the relative sizes of parasite
and host. However, grazing by nudibranchs on bryozoan colonies was dubbed partial predation by Harvell (1984), so concepts are fluid because authors do differentiate according to relative sizes of the consumer and the organism consumed.

Other words are now entering into English. Two useful ones are koinobiont and idiobiont [from Greek koinos (in common), idios (individual), and bios (life)] (Askew & Shaw 1986, modified from Haeselbarth 1979). A koinobiont is a parasitoid developing in a parasitized host which continues to be mobile and able to defend itself; larval hosts often are not killed until they have prepared cryptic pupation retreats. The host may not live very long after parasitism, but the koinobiont benefits from the continued life of its host. An idiobiont is a parasitoid which consumes the host in the location and stage it is in when attacked.

This symposium is not on the subject of behavioral ecology of predators and their prey, but our etymological voyage is incomplete without the following. The adjectives describing the distinguishing behavior of predators are predatory and predacious, also, erroneously, predaceous, cf. audacious, voracious, ferocious (OED 1971). Adoption of the spelling predaceous by Webster (1866) presumably is an acknowledgment rather than an endorsement of current erroneous spelling in North America. Perhaps some dictionaries of the last century acknowledged the spelling cocoa-nut as the name of the seed of Cocos nucifera L. (that spelling certainly was used), whereas today the etymologically more appropriate spelling coconut is accepted universally.

Before progressing to the chaotic future of behavioral ecology it is entertaining and perhaps illuminating to explore other writings from the past. These contain speculations which are not based on observation such as that by Drake. The principal character of a novel (Godwin 1688) of the mid-17th century, Domingo Gonzales, visited the moon, drawn there in an “engine” pulled by “gansans” [? geese] he had trained, during their annual migration. On the moon he found a fauna and flora different from that of earth, but including swallows and other migratory birds from earth. Intended only as a novel, it may have stimulated speculation in the mind of Charles Morton, a physician and philosopher (Harrison 1954).

Morton’s philosophical work (Morton ca. 1694) speculated on the disappearance of swallows and other birds each autumn and their return each spring: “... their chearefulness seems to intiate ... that they have some noble design in hand ... namely, to get above the atmosphere, hie and fly away to the other world ... till some other more fit place can be assigned, do go into and remain in some one of the celestial bodies; and that must be the moon, which is most likely, because nearest ... if the moon be not allowed, some other place must be found out for them.”

Morton thus recognized the disappearance of swallows as a migration, which was an advance on popular belief of that time. Popular belief was still being voiced some decades later, by no less an authority than Samuel Johnson (1768), in the following terms: “Swallows certainly sleep all the winter. A number of them conglobulate together, by flying round and round, and then all in a heap throw themselves under water, and lye in the bed of a river.”

Unfortunately, both worthies (Morton and Johnson) overlooked or ignored the earlier publication of a serious treatise on ornithology by Francis Willughby (1676), which included speculation on the migratory habits of swallows: “Quo abeant vel ubi latitent hirundines hyberno tempore, nec inter rei naturalis scriptores convenit, nec nobis sanc compertum est. Verisimilium tamen videtur eas in regiones calidiores Aegyptum putas aut Aethiopiam avolare ...” Willughby had speculated that swallows migrate to Egypt or Ethiopia in the winter. The later views on the subject by Morton (ca. 1694) and Johnson (1768) were in vain.

The past of behavioral ecology was fabulous. The beginnings of behavioral ecology’s explosive growth phase coincided with publication of Wilson’s Sociobiology (Krebs
1985). Studies of insects played key roles in both the early formation of behavioral ecology as a discrete subject and its subsequent rapid development (Burk 1988, Krebs 1985).

Krebs (1985) [see also Burk 1988] tabulated what he and a dozen colleagues thought were the most important developments in behavioral ecology during the decade 1975-1985. The areas of investigation they emphasized can be lumped into five categories relevant to insects: (1) game theory and alternative strategies, (2) optimization, (3) kin selection and kin recognition, (4) parental investment, and (5) communication and assessment. Krebs (1985), from his poll of colleagues, also endeavored to predict the immediate future courses of behavioral ecological research. Five paths were predicted: (1) life history and population dynamics in relation to behavioral ecology, (2) mating systems, (3) parasites and sexual selection, (4) learning, and (5) the genetic basis of behavior. Burk (1988), too, predicted five pathways for productive research, in behavioral ecology of insects: (1) sexual selection, (2) resource competition among females, (3) learning, (4) orientation and movement, and (5) communication.

One might infer, from comparing the two sets of predictions, that insect behavioral ecology lags in but a single area of research: communication. In other areas it seems to fit in with behavioral ecology of the rest of the animal kingdom. How do our symposium contributions fit in with predictions by Krebs (1985) and Burk (1988)?

Mike Strand's contribution details the reproductive behavior of a parasitoid, and examines its potential connection to competition for mates. Investigating mating systems is recognized by both Krebs (1985) and Burk (1988) as an important future course of behavioral ecological research. Two of the contributions (by Joe Lewis [with H.R. Gross, Jr.] and Jim Cronin [text not published here]) deal with the importance of environmental structure, especially vegetational types, on searching behavior of parasitoids. Burk (1988) emphasizes the important future role of studies of oriented movement in insect behavioral ecology. Dan Wojcik examines the myriad interactions between ants and their parasites and parasitoids, and questions previous generalizations about these interactions. His contribution raises an important point: future paths of behavioral ecology must lead from a solid foundation, lest we find ourselves swept up in a bocchanal of hollow theorizing (see Vehrenbaum & Bradbury 1984).

Two of the contributions (by Jon Allen, and Mike Antolin) concern genetic bases of behavioral interactions between parasitoids and hosts. Investigating the genetic basis of behavior is included explicitly in Krebs' (1985) tabulation, and is woven implicitly throughout Burk's (1988) discussion. Jon Allen's assertion that chaotic population fluctuations can result from density dependence is heartening to those of us who sometimes have tried in vain to see regularity in density dependent systems. Theory and practice come together here, in chaos.

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COMPARATIVE STUDIES ON FIELD PERFORMANCE OF HELIOTHIS LARVAL PARASITIDS MICROPLITIS CROCEIPES AND CARDOCHILES NIGRICEPS AT VARYING DENSITIES AND UNDER SELECTED HOST PLANT CONDITIONS

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ABSTRACT

Field performance of the Heliothis (Lepidoptera: Noctuidae) larval parasitoids Microplitis croceipes (Cresson) and Cardiochiles nigriceps (Viereëk) (Hymenoptera: Braconidae) was assessed at various parasitoid densities and on different plants. Laboratory-reared M. croceipes were released in field plots of soybeans and peanuts at levels of ca. 400 and 1,350/ha. Observed and calculated data indicate that over a 4-day period parasitism levels of 45 and 56%, respectively, would be obtained with M. croceipes at these levels on soybeans. Performance of M. croceipes on peanuts was less consistent, but in one study, 71% parasitism was obtained during a 2-day interval after releases of 1,344 females/ha.

The searching behavior and efficiency of C. nigriceps females were studied on the hyacinth bean (Dolichos lablab L.) and Florida beggarweed (Desmodium purpureum Mill.). Observed and calculated data indicate that populations of 9,622 and 5,371 females/ha on the hyacinth bean and beggarweed, respectively, would yield 80% parasitism, as compared to earlier studies showing that 988-1,142 females/ha yield this level of parasitism on cotton.

These findings show that the efficiency of the parasitoids varies considerably on different host plants. The distribution of searching parasitoids within the experimental plots and the distribution of their eggs among the host larvae did not differ significantly from a random (Poisson) pattern.

RESUMEN

Se evaluó en el campo el comportamiento de Microplitis croceipes (Cresson) y Cardiochiles nigriceps (Viereëk) (Hymenoptera: Braconidae), parasitoides de la larva de Heliothis (Lepidoptera: Noctuidae). En la evaluación se utilizaron varias densidades de parasitoides y diferentes especies de plantas. M. croceipes fueron criadas en el