Robert F. Denno (1945–2008): Insect Ecologist Extraordinaire

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Abstract

Robert F. Denno was widely recognized as one of the leading insect ecologists in the world. He made major contributions to the study of plant-insect interactions, dispersal, interspecific competition, predator-prey interactions, and food web dynamics. He was especially well known for his detailed and comprehensive study of the arthropods that inhabit salt marshes. Denno promoted a research approach that included detailed knowledge of the natural history of the study system, meticulous experiments that often pushed logistical possibilities, and a focus on important ecological questions of the day. He was an enthusiastic collaborator and excellent mentor who invested incredible amounts of time and energy in the training and placement of graduate students and postdoctoral associates. As a result, Denno's legacy will continue to shape the field of insect ecology for generations to come.

EARLY FOUNDATIONS OF AN INSECT ECOLOGIST

Robert Frederick Denno (1945–2008) was born in New York City but as a child moved to southern California. His love of natural history began in the foothills of California's coastal range near his home in Santa Barbara where much time was spent at La Cumbre Peak collecting insects. By the time he graduated from high school, Denno amassed 30 display drawers housing a large, meticulously curated collection of several hundred specimens of endemic butterflies, particularly checkerspots. This collection eventually swelled to over 36,000 specimens from around the world, housed in beautiful wooden cabinets that he crafted himself (**Figure 1**). His passion for science, ecology, and insects guided his curriculum choices through community college and as an undergraduate at the University of California at Davis. Denno graduated Phi Beta Kappa cum laude with a major in entomology and a minor in botany in 1967.

Figure 1

Robert Denno collecting butterflies in Arizona. Note the custom-built wooden specimen box and ever present diet Coke. Denno's lifelong passion for butterflies resulted in a meticulously curated personal collection of over 36,000 specimens.

Denno entered the doctoral program in the laboratory of an assistant professor, Dr. Warren Cothran, a dynamic member of the fledgling Insect Ecology group at Davis. Cothran's academic rigor, meticulous attention to detail, and rapport with students laid foundations that would become hallmarks of Denno's research and laboratory. Upon graduation in 1973, Denno began a postdoctoral appointment at Rutgers University, where he was first introduced to Atlantic coast salt marshes as part of a team studying the ecological effects of insecticides used in mosquito abatement programs. After only one year in this position, he was hired by Rutgers as an assistant professor of insect systematics, a testament to the breadth and depth of his knowledge of natural history. But his time at Rutgers was limited, as he was quickly lured away by the Department of Entomology at the University of Maryland, his home for the next three decades. Denno's original job description specified an emphasis on the management of insect pests of turfgrass, but he was encouraged to do the type of research that excited him. Over the course of his career, Denno became an internationally recognized figure in population and community ecology. He established a reputation for synthesis, with a talent for identifying broad patterns in nature and revealing their underlying mechanisms.

THE SEEDS OF COMPETITION

Denno's dissertation, completed in 1973, was entitled "Niche Relationships and Competitive Interactions of Carrion-Breeding Calliphoridae and Sarcophagidae" and resulted in two publications that provided the first examples of the comprehensive and in-depth writing style that was to become one of Denno's trademarks. Focusing on a foundational concept of competition theory, Denno addressed the Gaussian principle that no two species could occupy the same niche indefinitely (52). By manipulating periods of exposure and size of carcasses and measuring temporal patterns of exploitation, Denno & Cothran (14) provided evidence supporting Gaussian predictions that closely related species utilizing a similar resource diverged in patterns of utilization over several niche dimensions. Species of necrophagous flies differed in the size of carcasses used, seasonality, and stage of decomposition. Notably, in a theme that would recur in his monumental studies of insects inhabiting salt marshes, Denno & Cothran (14) found that the degree of specialization of carrion flies was linked to the stability of their food resources, with specialists utilizing stable resources and generalists utilizing less predictable resources. In a subsequent test, Denno & Cothran (15) found strong evidence of competitive release. Documenting and understanding patterns of resource utilization was a theme repeated by Denno in many systems including biting flies (109), aquatic insects (3, 4), spiders (39), tropical insects (16), and, most famously, salt marsh–inhabiting planthoppers (10, 12).

LIFE-HISTORY TRAITS AND WING POLYMORPHISMS

For more than three decades, Denno's primary focus was the community of arthropods inhabiting coastal salt marshes along the Atlantic Ocean and Gulf of Mexico. This ecosystem is dominated by relatively pure stands of the grasses *Spartina patens*, *S. alterniflora*, and *Distichlis spicata*. *D. spicata* and *S. patens* occupy higher elevations in the marsh, whereas *S. alterniflora* occurs at lower elevations and along creek banks. One striking feature of the herbivorous arthropods associated with these grasses is the widespread prevalence of wing dimorphism in guilds of sap-sucking Auchenorrhyncha, primarily leafhoppers and planthoppers. Many grasses are dominated by flightless, short-winged forms (brachypters), while some grasses house temporally and geographically shifting proportions of flight-capable, long-winged forms (macropters) (9, 10, 22).

Harlequin environment: insular patches of habitat that vary in quality or persistence occupied by species whose population dynamics and competitive interactions are governed by differential rates of colonization and extinction

Denno (9) predicted that brachyptery would prevail in denizens utilizing stable resources but that macroptery would characterize species occupying patchy or variable resources. Three species of planthoppers associated with the high marsh grass *S. patens* were strongly biased toward brachyptery. *S. patens* is a structurally uniform and spatially homogeneous resource with respect to patch quality. By contrast, at lower elevations the quality of *S. alterniflora* patches varied dramatically both spatially and temporally owing to variability in tidal inundation. Dimorphism in populations of *Prokelisia marginata* (**Figure 2**) was maintained by differing selective regimes in harlequin environments. Brachypters with limited dispersal capabilities were favored in stable patches, where they persisted and exploited *S. patens*, and macropters were favored in variable patches, escaping when resources declined in quality and colonizing others of higher quality. This model described shifting seasonal patterns in proportions of wing forms in populations of *P. marginata* during their annual interhabitat migrations between high- and low-quality patches of *S. alterniflora*, recolonization of defaunated patches of grass, and intraplant distributions as they exploited plant tissues of varying quality (9, 32).

Denno and colleagues (9, 11, 22) also proposed that a density-sensitive developmental switch triggered the production of macropters occupying variable host patches. Experiments designed to elucidate the mechanisms that trigger this switch found that developmental control of wing dimorphism in *P. marginata* was influenced by crowding, host nutrition, and their interaction, but crowding seemed to be the most important factor influencing wing development (17, 18, 26). Ideas spawned in *Spartina* systems culminated in a paradigm for

Figure 2

The Denno laboratory studied *Prokelisia* planthoppers and their cordgrass host plants in the genus *Spartina* for over 30 years. Here, two *P. marginata* planthoppers mate on *S. alterniflora*. Photographed by Dwight Kuhn.

wing dimorphism in planthoppers (35). In this study, levels of macroptery were strongly linked to habitat persistence in over 40 species of planthoppers. As habitat persistence declined, the proportion of migrants in the population increased.

Ecological forces underlying the evolution of migration in planthoppers were further revealed with the discovery of a second species of *Prokelisia*, *P. dolus*, inhabiting *S. alterniflora* (37). Unlike *P. marginata*, whose populations consisted of about 80% macropters, populations of *P. dolus* were composed of roughly 20% macropters. This species did not engage in annual interhabitat migrations on mid-Atlantic marshes. Different acoustic signaling and hybridization failure were two mechanisms isolating these sympatric species (57). This discovery and a lingering question regarding the adaptive significance of brachyptery were addressed in an important series of papers examining the cost of flight capability in planthoppers (29, 33). Using *P. dolus*, Denno et al. (29) demonstrated that female brachypters enjoyed enhanced fecundity, earlier age to first reproduction, and longer adult life than macropters. The pattern for greater fecundity and earlier reproduction in brachypters and enhanced dispersal abilities of macropters was documented in several species of planthoppers, confirming the trade-off between flight and reproduction (29, 33). Later studies confirmed that dispersal ability constrains reproduction in male *P. dolus* as well, with flight-capable macropterous males acquiring fewer matings and siring fewer offspring than their flight-incapable brachypterous counterparts (71). However, this dispersal polymorphism appears to be maintained in males, despite the fitness trade-off, because vegetation structure (sparseness) and low female density differentially favor macropterous over flightless males (72).

These ideas were confirmed in an exhaustive review of the wing polymorphism literature (116). Zera & Denno (116) reviewed studies of insects from nine orders to convincingly demonstrate that habitat persistence selects for reduced dispersal capability in insects. They also demonstrated that increased fecundity of flightless females is a remarkably widespread fitness trade-off found in almost all major insect orders.

Interspecific competition: competition for resources among individuals of different species

Denno's discovery of the coexistence of *P. marginata* and *P. dolus* provided an opportunity to return to questions regarding interspecific competition among closely related sympatric species. By rearing both species at different densities in isolation and together, Denno & Roderick found that interspecific crowding was as equally strong a stimulus for the production of migrants as intraspecific crowding (34). However, responses of the congeners to intraspecific crowding were asymmetrical. Intraspecific crowding resulted in delayed development, reduced body size, and lower survival in *P. marginata*, but not in *P. dolus*. Because of its profound effects on the reproduction and fecundity of *P. marginata*, interspecific competition emerged as an important selective force in this system by increasing emigration and decreasing population growth of planthoppers inhabiting *S. alterniflora* (34).

INTERSPECIFIC COMPETITION

Denno's growing awareness of the importance of interspecific competition in the population dynamics of *Prokelisia* planthoppers (34) led him to contemplate the broader importance of interspecific competition in ecology. During the 1960s and 1970s, interspecific competition was assumed to be an important force affecting the distribution, abundance, and community structure of herbivorous insects, although this view developed largely as a result of observational studies (5, 101). During the late 1970s and early 1980s, however, the presumed importance of competition on the structure of phytophagous insect communities was severely challenged and within a few brief years the prevailing view was that interspecific competition was weak and infrequent (76, 77, 105). These critiques of interspecific competition, in turn, stimulated many well-executed, experimental evaluations of the importance of competition among herbivorous insects. Many of these studies were published in the late 1980s and early 1990s. Denno et al. (28) immersed themselves in this literature and extracted data on 193 pairwise species interactions occurring in 104 different study systems. The majority of these pairwise interactions (148 in total) were experimental assessments of competition. Denno et al. found that interspecific competition was incredibly widespread: Seventy-six percent of the pairwise interactions showed strong evidence of competition, whereas only 18% of the interactions indicated an absence of competition and 6% supported facilitation. This remarkably comprehensive evaluation of the literature was extremely influential. The review has been cited 296 times to date and has definitively changed the way insect ecologists view competition.

In the ten years following Denno's original review of competition, the growing body of literature reflected a greater emphasis on indirect interactions including plants (i.e., induced defenses) and natural enemies (i.e., apparent competition). Given this shifting focus, Kaplan & Denno (62) revisited the issue of competition, this time using a quantitative meta-analytical approach to assess whether herbivorous insects conform to the traditional paradigm of interspecific competition. Notably, they found that indeed interspecific competition was common, but that many widely held assumptions did not hold. Specifically, there was no correlation between the amount of plant damage and the intensity of competition, competition occurred between distantly related species in different feeding guilds, it was not dampened by temporal or spatial resource partitioning, and it was highly asymmetric. These results point toward a significant contribution of indirect interactions, whereby plants and/or natural enemies mediate competitive interactions among herbivores. Kaplan & Denno concluded that, to understand how interspecific competition contributes to the organization of phytophagous insect communities, a new paradigm that accounts for indirect interactions and facilitation is required (23, 62).

Several studies emerged from Denno's laboratory that provided support for the prevalence of indirect interactions among herbivorous insects that partition their resources either temporally or spatially. For example, Denno et al. (31) found that early-season feeding by *P. dolus* on *S. alterniflora* grass in high marsh meadows induced changes in plant quality that negatively affected populations of *P. marginata* colonists that arrived later in the season. Lynch et al. (82) also found that previous feeding by potato leafhoppers, *Empoasca fabae*, resulted in adverse plant-mediated effects on later-feeding Colorado potato beetles, *Leptinotarsa decemlineata*, such as reduced survivorship and delayed development. This induced resistance to early-feeding leafhoppers in turn enhanced the

Indirect interactions: one species influences a second species by virtue of its impacts on an intermediary species

Induced defenses: dynamic plant defenses that are produced in response to attack by insects

Apparent competition: one prey species has an indirect negative effect on another prey species via its direct positive effect on the abundance of a shared predator beetle's risk of predation because its slowed growth increased exposure to predators during susceptible stages (65). Spatially segregated herbivores that feed above- and belowground on the same host plant also interact, due to the physiological integration of root and shoot defense (63, 64, 66). Nematode herbivory of tobacco roots interferes with the defensive induction of the plant, positively influencing aboveground-feeding phytophagous insects. Likewise, aboveground-feeding herbivores facilitate plant parasitic nematodes by stimulating plants to allocate nutritional reserves to the roots.

VARIABLE PLANTS AND HERBIVORES

With recognition that planthoppers closely tracked high-quality resources at several spatial scales, plant nutrition as a determinant of herbivore behavior and population dynamics became an organizing theme in Denno's laboratory (32). Several graduate students embarked on studies of how variation in plant resources affects plant and herbivore interactions.

In one set of studies, phenological and sex-based variation in plant quality influenced herbivore feeding behavior. Along the upper fringes of the salt marsh grows the dioecious woody shrub *Baccharis halimifolia*. *B. halimifolia* has a specialized chrysomelid beetle, *Trirhabda bacharidis*. Kraft & Denno (68) found that young foliage was preferred by these beetles and that the beetles performed better when fed young foliage. Sex ratios of *B. halimifolia* were slightly female biased (~60%) in natural settings. Krischik & Denno (69, 70) found that *T. bacharidis* and a polyphagous flea beetle, *Paria thoracicai*, preferred to feed on male plants owing to a greater abundance of tender young leaves on rapidly growing male plants.

The defensive strategy of the host plant was also determined to affect the feeding behavior and host utilization of phytophagous insects. One widespread defensive syndrome in terrestrial plants is to arm secretory canals with noxious resins, gums, muscilages, or latexes. Some phytophagous insects are behaviorally adapted to preempt these defenses by cutting or trenching veins or canals that supply and distribute these defenses. By examining feeding behaviors of 33 species of caterpillars, beetles, and katydids on canal-bearing plants, Dussourd & Denno (40) found that distinct patterns emerged across widely disparate plant lineages. Regardless of the taxonomic affinity of the herbivores, there was a close link between feeding behavior and the architecture of secretory canals. Phytophagous insects that consumed plants with secretory canals prevented the flow of secretion to distal branches of the canals by cutting the major leaf veins, thereby rendering much of the leaf defenseless. Alternatively, herbivores that fed on plants with net-like anastomosing canals transected all strands of the network by cutting a trench in the leaf. Thus, diverse insects that successfully attack these plants employ the same behavior on similar canal architectures, even when their host plants otherwise differ in taxonomy and secondary chemistry (40).

In one of the earliest tests of the importance of inducible plant defenses, another chrysomelid, *Plagiodera versicolora*, was used to examine changes in host suitability in *Salix* following natural and artificial defoliation. Leaves damaged artificially by tearing or naturally by the feeding of mandibulate herbivores resulted in a ~20% reduction in the fecundity of *P. versicolora*. Furthermore, damage to one leaf reduced the suitability of adjacent undamaged ones as evidenced by reduced weight and slower development of leaf beetle larvae (96). Willow beetles were later shown by other investigators to deal with altered leaf quality by avoiding previously damaged leaves (97).

Denno's laboratory was also interested in how host plants mediated the effects of natural enemies on herbivores. Willow beetles provided an excellent model for examining patterns of host utilization and dietary breadth in the context of enemy-free space (24). Larvae of *Phratora vitellinae* produced defensive secretions from precursors found in leaves of their host, whereas larvae of another willow-feeding leaf beetle, *Galerucella lineola*, lacked this ability. Female *G. lineola* selected and oviposited on willow species where larval performance was greatest. By contrast, *P. vitellinae* oviposited on hosts of varying quality for larvae but preferred hosts rich in precursors for larval defensive secretions. In the presence of predators, the ability of these beetles to produce potent defensive secretions outweighed costs associated with slower development and lower survival on suboptimal hosts. The role of enemy-free space in shaping dietary breadth and specialization in these leaf beetles provides some of the clearest support for this hypothesis (24).

Benrey & Denno (1) further explored the effects of host plants on herbivore–natural enemy interactions by testing the slow-growth/high-mortality hypothesis. This hypothesis predicts that prolonged development on poor-quality hosts results in increased exposure to natural enemies and a subsequent increase in mortality. They conducted a series of experiments to determine how host plant species influenced the larval development of imported cabbageworm, *Pieris rapae*, and their vulnerability to attack by the parasitoid wasp *Cotesia glomerata*. They found that rapidly developing caterpillars reached instars that were invulnerable to attack faster and thus had a shorter "window of vulnerability" than slowly growing caterpillars. Consequently, caterpillars reared on relatively poor-quality host plants suffered significantly higher levels of parasitism. This was true, however, only within a given host plant species. Parasitism rates among plants were largely specific to the plant species and not explained by development time of caterpillars. These studies were extremely influential because they demonstrated that plants can increase the susceptibility of insect herbivores to natural enemies via multiple mechanisms and that these indirect effects can have important consequences for the ecological and evolutionary interactions of plants and insects.

Ultimately, Denno's laboratory documented that variability in host plants can have community-wide impacts on the trophic structure, composition, and diversity of an entire arthropod food web (115). Increasing *S. alterniflora* biomass production on the salt marsh by enhancing nutrient inputs resulted in an increase in the species richness of herbivores, detritivores, predators, and parasitoids, primarily due to an increase in the diversity of rare species. In addition, there were significant changes in arthropod species composition with increasing levels of production (115).

Although the vignettes described above provide a sample of his work, Denno's interests in the grand sweep of plant variation and the evolutionary and ecological responses of herbivorous insects crystallized in an early, remarkable treatise, *Variable Plants and Herbivores in Natural and Managed Systems* (27). Co-edited with his lifelong friend Mark McClure, the "green book," as it was known to many insect ecologists because of its bright green cover, is a classic synthesis of the evolutionary ecology of plant-herbivore interactions and remains a foundational work in plant-herbivore theory.

EVOLUTIONARY AND ECOLOGICAL TRADE-OFFS

Evolutionary trade-offs between reproduction and migration in planthoppers led to investigations of evolutionary trade-offs in other systems. In a series of fascinating studies with his student, Douglas Tallamy, Denno investigated another type of life-history trade-off: the trade-off between maternal care and reproduction in the eggplant lace bug, *Gargaphia solani*, a specialist on solanaceous weeds. Following the discovery that female *G. solani* defend their nymphs from predators but do not assist in feeding or locating resources, trade-offs between egg production, maternal care, and longevity were quantified (107, 108). Maternal care significantly reduced female fecundity, but the disadvantages of mothering were strongly offset by greatly enhanced survival of offspring when mothers protected progeny from predators. Thus, maternal care increased fitness and longevity of females (107, 108).

Interests in energetic trade-offs of differing life-history traits led to an examination of costs and benefits of fecal shields in chrysomelid tortoise beetles. As larvae, many species of tortoise beetles collect feces and exuviae on modified caudal appendages. Three species of tortoise beetles, *Charidotella bicolor*, *Deloyala guttata*, and *Chelymorpha cassidea*, were raised under laboratory conditions with their fecal shield intact or removed. Removal of shields in the absence of predators did not affect performance of larvae and resulted in no compensatory feeding to build replacements. However, in laboratory settings, fecal shields deterred small predators with piercing mouthparts, such as *Geocoris*, and mandibulate predators, such as coccinellids. Tortoise beetles suffered high mortality in natural settings when fecal shields were removed, leading to the conclusion that fecal shields provided a low cost but potent defense to their chrysomelid bearers (86, 87).

Genetic isolation by distance: because neighboring populations are more likely to exchange genes, genetic exchange among populations of species with limited dispersal ability may be strongly correlated with geographic distance among populations

Plant stress hypothesis: drought promotes outbreaks of phytophagous insects because nitrogen availability is increased in water-stressed plants

EVOLUTIONARY CONSEQUENCES OF VARIATION IN DISPERSAL ABILITY

Denno's work with wing-dimorphic planthoppers that differed dramatically in their dispersal abilities stimulated an interest in the evolutionary consequences of this variation. Denno and his colleagues predicted that flightless insects should show much stronger population differentiation than their winged kin. Peterson & Denno (90) tested the hypothesis that levels of gene flow among planthopper populations were correlated with wing form (dispersal ability). They found that in both *P. marginata* and *P. dolus*, population-genetic subdivision was strongly correlated with dispersal ability, such that subdivision decreased as the level of macroptery increased. Peterson & Denno (91) expanded on this question by reviewing the literature on genetic isolation by distance for 43 species and host races of phytophagous insects. Somewhat surprisingly, they found that genetic isolation by distance was weak in sedentary as well as highly mobile species. They concluded that genetic isolation by distance was weak in strong dispersers because of the homogenizing effects of gene flow and that genetic isolation by distance was weak in sedentary insects because reduced gene flow resulted in population differentiation among virtually all populations. The strongest genetic isolation by distance was found in species with moderate dispersal abilities because modest dispersal creates genetic homogeneity at relatively small scales but significant divergence over longer distances. Peterson & Denno also used this data set to test and ultimately refute the long-standing hypothesis that genetic isolation by distance increases as diet specialization of phytophagous insects increases. Genetic isolation by distance did not differ among monophagous and polyphagous herbivores, casting serious doubt on the idea that diet specialization promotes diversification by influencing population-genetic subdivision.

EFFECTS OF PLANT STRESS ON HERBIVORE DYNAMICS

Entomologists have been interested in the effects of plant stress, especially drought stress, on herbivore population dynamics for nearly a century (8, 85). In many cases, stress from lack of water, altered nutrient availability, heat, shading, and flooding is correlated with insect outbreaks (112). By contrast, many herbivorous insects perform better on unstressed plants (67), and it has been a challenge for insect ecologists to reach a consensus about the effects of stress on the susceptibility of plants to insects (75, 85, 98). Within this context, Hanks & Denno (56) set out to determine the relative effect of drought stress on outbreaks of pests on urban trees. Hanks & Denno found that the distribution of the white peach scale, *Pseudaulacaspis pentagona*, on mulberry trees at urban sites and forested sites was determined by an interaction of water stress and natural enemies. Water potential is inversely related to water stress, and water potential of mulberry trees at forested sites was significantly higher compared to that of trees at urban sites. Water potential was positively correlated with the survival of scales, suggesting that scales should be most abundant on unstressed plants like those found at forested sites. Surprisingly, armored scales were actually more abundant at urban sites than at forested sites. Generalist natural enemies like phalangids, earwigs, and tree crickets were much more abundant at forested sites, and these generalist predators strongly reduced the survival and subsequent abundance of scales. Consequently, scales were largely relegated to the subset of mulberry trees at urban sites that were not water stressed and where generalist predators were rare.

In a similar study, Trumbule et al. (111) found that azalea lace bugs, *Stephanitis pyrioides*, were more abundant and caused more damage to azalea plants that were in stressful locations that received high light and low water. Subsequently, Trumbule & Denno (110) tested the hypothesis that azaleas grown under high light intensity and low water availability are stressed and promote lace bug outbreaks. In a series of greenhouse and field experiments, survival of caged azalea lace bugs was higher and female lace bugs were more fecund and preferred to feed and oviposit on shade-grown, well-watered azaleas rather than on azaleas grown in full sun with limited water, results all counter to the hypothesis. When they placed uncaged lace bugs on plants, however, lace bug survival was dramatically lower on plants in shaded woodlot habitats than on plants in open settings. Trumbule & Denno hypothesized that although shaded and watered azaleas were better host plants for lace bugs, generalist predators were more abundant in shaded habitats and were responsible for strong lace bug suppression. Subsequent work in this system confirmed this hypothesis (102).

Denno also investigated the effects of plant stress on herbivore dynamics in his beloved salt marsh system. Huberty & Denno (59) found that the closely related, phloem-feeding planthoppers *P. marginata* and *P. dolus* responded differently to plant stress. Huberty & Denno found that both planthoppers performed best when they were reared on luxuriant *Spartina* plants that were supplied with optimal levels of nitrogen and phosphorus. When plants were nitrogen stressed, the performance of *P. marginata* planthoppers was dramatically reduced, whereas the performance of *P. dolus* planthoppers was only slightly affected. *P. marginata* planthoppers were also negatively affected when plants were phosphorus stressed, although not to the same extent as when plants were nitrogen stressed. *P. dolus* planthoppers, however, were not affected at all when grown on phosphorus-stressed *Spartina*. Huberty & Denno (60) demonstrated in a companion study that *P. dolus* planthoppers avoid the effects of plant stress because they have significantly larger cibarial muscles that allow them to pump more phloem from their host plants than *P. marginata* planthoppers do. Huberty & Denno argued that these two species evolved divergent strategies for dealing with stressed host plants: The typically macropterous *P. marginata* invests in the flight musculature necessary to disperse from patches of stressed plants where it performs poorly, whereas the typically short-winged *P. dolus* invests in the cibarial musculature necessary for compensatory feeding.

In most of these cases, Denno and his students found that unstressed, vigorous plants were better hosts for herbivores, even though herbivore abundance was often not solely dictated by host plant quality, and some herbivores have strategies for dealing with stressed plants. Given Denno's penchant for synthesis, it is not surprising that Denno was driven to compare and integrate the results of work conducted by his laboratory with the work of other ecologists. Huberty & Denno (58) used data from over 80 published studies to test the hypothesis that drought stress increases herbivore performance and promotes outbreaks. They found that the performance and population growth of sap-feeding insects (those that feed on xylem, phloem, and mesophyll) and insects that induce galls were much lower on water-stressed plants than on unstressed plants. Furthermore, borers were the only insects that consistently benefited from feeding on water-stressed plants. The results of this review were surprising and profoundly challenged the long-held view that water stress promotes outbreaks of insect herbivores.

OMNIVORY

Denno had a long-standing interest in the evolution and ecological consequences of omnivory (feeding at more than one trophic level). In particular, Denno was interested in identifying factors that promote the evolution of omnivory and understanding the consequences of omnivory for omnivore-resource interactions. Denno & Fagan (19) took an extremely broad view of the evolution of omnivory and proposed that the mismatch in nitrogen stoichiometry between herbivores and their host plants and differences in nitrogen content between predators and their herbivorous prey promote omnivory. Basically, Denno & Fagan hypothesized that nitrogen-limited arthropods could enhance their nitrogen intake by broadening their diet to include nitrogen-rich prey. This extremely compelling paper strongly influenced how ecologists view (55, 114) and study nitrogen limitation in arthropods (84). As a result, there has been a greater integration of the nutritional requirements of secondary consumers in the study of ecological interactions (94) and critical evaluations of our assumptions about these nutritional requirements (113).

In a more detailed evaluation of the evolution of omnivory within a single group of insects, Eubanks et al. (44) focused on terrestrial lineages of the insect suborder Heteroptera and tested the idea that feeding on nitrogen-rich plant parts and polyphagy are correlated with the evolution of omnivory in this group. Feeding on high-nitrogen plant parts (seeds and pollen) and polyphagy were strongly associated with the evolution of omnivory within ancestrally herbivorous lineages and, likewise, omnivores that evolved within ancestrally predaceous lineages typically fed on nitrogen-rich plant parts of many different host plants. Results of this study and work on a wide range of other animals strongly suggest that omnivores that feed on both plants and prey represent a unique blend of adaptations found in their predaceous and herbivorous relatives (6, 7).

Denno's laboratory group asked questions about the ecological significance of omnivory in multiple study systems. Eubanks & Denno (42, 43) investigated the ecological consequences of omnivory in lima beans by the big-eyed bug, *Geocoris punctipes*. High-quality plant food, in this case lima bean pods, significantly increased the survival of big-eyed bug nymphs fed low-quality prey (pea aphids). Feeding on lima bean pods also allowed big-eyed bug nymphs to survive long periods without prey, and dispersal of big-eyed bugs was dramatically reduced by the presence of pods on plants. Not surprisingly, big-eyed bug populations were significantly larger in plots of lima beans with pods than in plots of lima beans without pods (42). Although the presence of pods acted as an alternative prey that reduced the per capita consumption of aphids and moth eggs by big-eyed bugs, the dramatic increase in the abundance of big-eyed bugs associated with pod feeding resulted in higher total prey consumption (43). Similarly, Frank et al. (51) found that adding grass seeds to cornfields could significantly decrease the incidence of cannibalism in omnivorous ground beetles and thus potentially lead to greater pest suppression. One of Denno's last students, Rachel Pearson, found that the salt marsh katydid, *Conocephalus spartinae*, was highly omnivorous and that in the field this katydid tracked variation in plant quality rather than changes in prey abundance, even though prey abundance affected its fitness to a greater extent than variation in plant quality (89).

HETEROGENEOUS HABITATS AND SPECIES INTERACTIONS

The role of habitat heterogeneity in mediating species interactions and shaping community structure was a recurring theme of Denno's work that was examined at a variety of dimensions and spatial scales. Despite the superficial appearance of a uniform habitat, salt marsh habitats are actually extremely heterogeneous due to the influence of tidal inundation on the accumulation (or lack of accumulation) of dead plant material, thatch, at the base of marsh plants. Denno (10) evaluated the impact of thatch on the diversity and composition of phytophagous insect communities by comparing the assemblage of sap-feeders inhabiting structurally complex *S. patens* with its dense matrix of associated thatch and sap-feeders found in the less complex vegetation of *S. alterniflora*. Species richness, diversity, and evenness were greater in *S. patens*. Denno (10) altered the structure of *S. patens* by removing its thick layer of thatch, thereby homogenizing the habitat. Habitat homogenization resulted in lower diversity and evenness of associated sap-feeders. In a related study, another species of salt marsh grass, *D. spicata*, yielded similar results. Owing to a dense accumulated layer of thatch and upright culms that support a tangle of leaf blades, *D. spicata* was much more architecturally complex than *S. alterniflora*. Correspondingly, the community of sap-feeders was richer and more diverse in *D. spicata* than in *S. alterniflora* (106).

A comprehensive study of spider communities in cordgrass habitats varying in thatch abundance and architectural complexity revealed a role for habitat heterogeneity in structuring communities at higher trophic levels as well (39). *S. patens* had a less diverse community of spiders than S. *alterniflora*, and *S. alterniflora* at high elevations housed a greater diversity of spiders than *S. alterniflora* along creeks, where inundation and seasonal destruction of the grass occurred. *S. alterniflora* provided architecture sufficient for colonization by web-builders that was lacking in *S. patens*, whereas the community of spiders in *S. patens* was dominated by hunting spiders (39). Langellotto & Denno (73) determined if this was a broad pattern in nature by performing a meta-analysis of the relevant literature. They found that the aggregation of predators in complex habitats is a generalized response across predatory taxa, including hunting and web-building spiders, hemipterans, mites, and parasitoids (73). The mechanisms underlying this response were poorly known in most cases, but further experiments on the marsh found that the presence of thatch provided refuge for spiders from cannibalism (74) and diminished the occurrence of intraguild predation (45, 46). Thus, complex-structured salt marsh habitats appear to promote spider abundance by both promoting their accumulation and enhancing their survival once they arrive.

Intraguild predation: predators consume other predators with which they compete for a shared prey resource

At a larger spatial scale, habitat heterogeneity in the form of host plant patches that vary in size and isolation was also found to influence herbivore communities and their interactions with natural enemies. Due to subtle differences in elevation on the marsh surface, *S. patens* often occurs in relatively large pure stands or as smaller patches or islands embedded in a matrix of *S. alterniflora*. Raupp & Denno (95) found no differences in species richness between small and large patches but discovered lower abundance of several species of sap-feeders on small habitat patches (12, 95). More recently, ecological traits such as mobility and fecundity of *S. patens* inhabitants were linked with critical habitat thresholds using 62 patches of *S. patens* spanning four orders of magnitude of patch size (83). Specialists and poor dispersers were highly influenced by spatial structure, but these factors had little effect on generalists and highly mobile species.

POSITIVE PREDATOR-PREDATOR INTERACTIONS

Although negative interactions among predators (intraguild predation) was a frequent focus of Denno's research (19, 45, 47, 49, 74), his laboratory also found that positive predator-predator interactions could play an important role in community dynamics. Losey & Denno (80) found that aphid suppression in alfalfa was dramatically increased when aphids were exposed to a combination of foliar-foraging predators (lady beetles) and ground-foraging predators (ground beetles) than when exposed to either predator alone. This synergistic suppression of aphids occurred because aphids dropped from plants in response to foliar-foraging predators (81), a behavior that made them accessible to ground-foraging predators

Top-down: natural enemy-mediated regulation of herbivore populations

Trophic cascade: an indirect effect of natural enemies on plants transmitted by the direct effect of enemies on herbivores

Bottom-up: plant-mediated regulation of herbivore populations

(79). This study was one of the first to document synergistic effects of invertebrate predators on their prey and was a forerunner of more recent studies that have shown positive effects of increasing predator diversity, especially functional group diversity, on herbivore suppression (50, 93).

FOOD WEB COMPLEXITY AND TROPHIC CASCADES

In the 1990s and early 2000s considerable dispute raged in the ecological literature on whether the top-down effects of natural enemies on herbivores were strong enough to cascade down through the food web to indirectly benefit primary producers (104). For terrestrial food webs dominated by phytophagous arthropods, there was accumulating support both for and against the occurrence of such trophic cascades (99), but a synthesis of the factors underlying these disparate findings was lacking. Finke & Denno (47, 49) approached the issue from a mechanistic perspective, attempting to explain why enemy effects cascade in some situations and not others. They conducted a series of field and greenhouse studies with the salt marsh community, examining the interactive effects of predator diversity, the presence of intraguild predators, and habitat complexity on the occurrence of trophic cascades. Increasing predator diversity dampened cascading effects of natural enemies on *Prokelisia* planthoppers and *S. alterniflora* cordgrass biomass (47, 48), but this effect was mediated by the presence of intraguild predators. As the proportion of intraguild predator species in the predator assemblage increased, the strength of the trophic cascade decreased. Therefore, a reticulate food web with high predator diversity and complex trophic interactions (e.g., intraguild predation) buffered the community against the occurrence of a trophic cascade. These studies were among the first to examine the cascading responses of herbivores and plants to manipulated diversity within the predator guild (rather than merely the presence/absence of predators), and they remain one of the most comprehensive mechanistic examinations of the effects of predator diversity loss on prey suppression and plant biomass (2, 100, 103).

TEMPORAL AND SPATIAL VARIATION IN TOP-DOWN AND BOTTOM-UP FACTORS

While some might find it tedious to work in the same system for over 30 years, Denno's in-depth studies of planthopper ecology gave him the unique perspective necessary to develop a mechanistic understanding of the complex, larger-scale processes governing the dynamics of the terrestrial salt marsh food web. As a result, he synthesized his extensive work on planthopper population dynamics; life-history strategies; species interactions such as competition, omnivory, plant-herbivore, predator-prey, and predator-predator interactions; and the mediating effects of habitat heterogeneity to explain temporal and spatial variation in the relative strengths of bottom-up (host plant resources) and top-down (predation) forces on phytophagous insects and their subsequent cascading effects on plant biomass. In a comprehensive approach that was a hallmark of Denno's experimental style, he integrated a series of manipulative studies from the laboratory and field with extensive sampling of field populations to develop a conceptual model of the processes at work on the salt marsh. What emerged was a general paradigm in this system of bottom-up primacy, whereby plants set the dynamic stage on which herbivorous insects and their natural enemies interact (21).

What Denno described was the existence of a landscape gradient across the salt marsh in the quality and structure of basal resources and the abundance of natural enemies that leads to spatial variation in the relative strength of top-down and bottom-up forces. Marsh habitats at lower elevations are characterized by nitrogen-rich *Spartina* that is free of thatch due to frequent tidal inundation that deposits nutrients and removes plant debris (13, 39). The high nitrogen content of the low-marsh *Spartina* promotes mass colonization, enhances survival and fecundity, and encourages rapid population growth of *Prokelisia* planthoppers (30, 88). At the same time, the paucity of thatch and greater tidal disturbance combine to reduce populations of many predators including *Pardosa* wolf spiders (39). The rarity of natural enemies, coupled with superior *Spartina* nutrition, promotes the largest planthopper populations and fosters outbreaks (30). Thus, Denno concluded that bottom-up forces generally prevail at lower elevations on the marsh.

In contrast, invertebrate predators play a greater role in planthopper suppression in certain high-elevation marsh habitats characterized by nitrogen-poor plants with abundant thatch. Impacts of natural enemies are more pronounced in these high-marsh habitats because the colonization-enhancing and growth-promoting effects of host plant nutrition on planthopper populations, and thus the opportunity for escape from control by predators, are not as strong. In addition, thatch encourages predator aggregation (38) and diminishes antagonistic predator-predator interactions such as cannibalism (74) and intraguild predation (45), increasing the overall abundance of predators. However, the top-down impact of natural enemies is mediated not only by host plants, but also by the identity of the herbivores themselves, with both defensive/escape behaviors and life-history strategies playing a role (20, 30). Predators play a more prominent role in the suppression of *Prokelisia* planthopper populations than other sap-feeders on the marsh, due in part to the ineffectiveness of the *Prokelisia* defense/escape response (20). Even between the two *Prokelisia* species, the relative strength of top-down effects also varies, mediated by differences in their life-history strategies. The highly mobile *P. marginata* planthoppers colonize nutritious host plants in very high numbers (13, 36), and in so doing, partially escape natural enemy impact (21). The less mobile *P. dolus* planthoppers are more susceptible to suppression by predators because their reduced dispersal ability delays their population response to nitrogen-rich plants.

But plant factors not only influence the strength of predator impacts on planthopper populations, they also dictate when such impacts are realized. Gratton & Denno (53) showed that *Prokelisia* planthoppers in habitats with high-nitrogen *Spartina* experience a temporal shift from population increases promoted by bottom-up processes during the summer to strong top-down suppression later in the season. The greater impact of natural enemies at the end of the season, despite the direct positive effects of nutrition on planthopper colonization and growth, is the result of a buildup of predators over the season. This buildup is the result of direct effects of habitat complexity on predator aggregation and retention and indirect effects on the availability of alternative prey.

Lewis & Denno (78) added an additional layer of complexity to this increasingly complicated picture by considering how spatial subsidies of predators interact with variation in host plants and resident natural enemies to influence populations of insect herbivores. They documented an annual spring/summer migration of *Pardosa* wolf spiders out of their overwintering habitat in upland *S. patens* into *S. alterniflora*, which results in a decline in *Pardosa* abundance with increasing distance from *S. patens* (25, 78). Because *Pardosa* is a voracious intraguild predator, this subsidy shifts the composition of the predator community, such that intraguild predators dominate the predator assemblage near *S. patens* and their impacts decline with increasing distance from *S. patens* patches. Thus, the opportunity for antagonistic interactions among predators also decreases with increasing distance from *S. patens*. However, the biomass of thatch is also greatest nearer *S. patens*, providing refuge from intraguild predation, promoting predator accumulation, and enhancing top-down control of planthoppers and their cascading effects on plants (38, 45, 74).

When Denno began his synthesis of factors influencing planthopper populations on the marsh, the historical controversy over the importance of top-down versus bottom-up impacts on phytophagous insect populations (41, 54) had already been supplanted by a more unified view (27, 61, 92). Therefore, the significance of Denno's contribution to this field comes not from his recognition that host plant factors can mediate the intensity of natural enemy impacts on herbivore populations, but from his identification of the larger-scale spatial and temporal patterns and his ability to provide a mechanistic explanation for why the patterns exist. Years of independent studies on the intricacies of individual species interactions provided the pieces of a puzzle that Denno, given his intimate knowledge of the system and knack for synthesis, was uniquely able to assemble into a complete picture.

A HOLISTIC VIEW OF DENNO AND HIS CAREER

Although Robert Denno loved butterflies, western plants, and diverse habitats, his research focused on a relatively nondiverse and simple system for almost 40 years. He kept his work fresh and relevant by incorporating the latest hot topics in ecology, be it top-down versus bottom-up regulation of populations, intraguild predation, or stoichiometry. Denno also kept his work fresh by having graduate students that worked outside the marsh, often focusing on plants of agricultural and landscape importance. This helped him intimately learn the insects and plants of many systems and explore diverse research questions without altering his own focus. Denno often expanded his research horizons by synergizing his interests with those of new students, postdocs, and visiting scientists (e.g., population geneticists). Denno made the most out of his travels and managed to conduct several significant research projects while leading field courses or visiting colleagues in a variety of places (e.g., Sweden, Costa Rica, Venezuela, Mexico, British Virgin Islands).

Denno's accomplishments as a scientist and a person were the direct result of his partnership with his wife of 42 years, Barbara Denno. They first met at a football game during their senior year of high school and were inseparable thereafter. Barb provided the intellectual and moral support that sustained Denno's career. But she also contributed directly to his research program by counting thousands (if not millions) of planthoppers, performing literature searches and tracking down citations, organizing his trips to meetings and other functions, and quelling his frustration over the disappearance of DOS-based word processing programs and minor computer glitches. The Dennos welcomed students, friends, and colleagues into their home. Parties at the Denno home were often fueled by rum and diet coke and full of thought-provoking discussions and tons of laughter and camaraderie. Bob was never known to take himself too seriously and he knew how to have a great time.

His synthetic approach to ecology and his ability to provide a complete story meant that Denno's talks at meetings were inevitably standing room only. This was despite (or perhaps because of) Denno's unconventional style of writing talks word-for-word beforehand and many, many, many practice sessions. This meticulous approach to public speaking resulted in Denno knowing exactly what he wanted to say, using precisely the right words, and packing more than seemingly possible into the allotted time.

Denno was an unmistakable force in insect ecology, not only because of the quality of his research, but also for his dedication to mentoring and the desire to make science a social endeavor. He was famous for his impromptu gatherings at scientific meetings where graduate students were welcomed and encouraged to interact with established scientists. When on departmental seminar visits, he devoted as much (if not more!) attention to discussions with students than he did with faculty members. His commitment to the training and promotion of his own students was unwavering, famously promising one future graduate student on his interview visit that "my job is to get you a job." In the end, Denno measured his own success not by the number of papers he published, but by his academic lineage of students and postdoctoral associates, of which there were many.

Denno's laboratory worked on an array of topics in insect ecology. Yet the majority of these studies included a deep understanding of the natural history of the system, a detailed, meticulous experimental approach, and a strong focus on synthesizing the results of research in that area. We hope that those who read this review, especially students, get a sense of the depth and breadth of Denno's research and the passion that he brought to science and to scientists. His deep commitment to digging deeper into his study system, to telling complete stories, and to developing future ecologists means that Denno's legacy will continue to shape the field of insect ecology for generations.

SUMMARY POINTS

1. Spatial and temporal heterogeneity of resources dictates the richness, diversity, and abundance of arthropod communities in a variety of habitats. Architecturally complex habitats and resource patches that vary spatially and temporally in quality provide opportunities for coexistence in diverse assemblages of herbivores and their natural enemies by relaxing competitive interactions and reducing effects of top-down forces. Specialization is often positively linked to the persistence of resources.
2. Herbivorous insects employ a variety of behavioral, physiological, and morphological adaptations to counter plant defenses, evaluate nutritional variation in their hosts, and mitigate attack from enemies. Strategies such as flightlessness, vein-cutting, and host and tissue specialization are widely distributed across insect taxa, whereas other strategies such as maternal care and the use of morphological shields against predators may be less widespread.
3. Habitat persistence selects for reduced dispersal capability in many insects because insects trade-off higher investment in reproduction with investment in the musculature associated with flight. Wing polymorphisms in which some individuals of a species do not produce fully functioning wings and flight muscles and some individuals do are a common form of reduced dispersal ability in insects.
4. Interspecific competition is an important ecological force that influences the population dynamics and community structure of phytophagous insects. Host plants mediate interspecific competition more frequently than natural enemies, physical factors, and intraspecific competition. The intensity of interspecific competition is not correlated with plant damage, can occur between distantly related species, is not dampened by temporal or spatial resource partitioning, and is often asymmetric.
5. Plant stress caused by lack of water often leads to reduced herbivore performance and smaller populations of herbivores. This occurs in a wide range of plants that inhabit diverse habitats and across many insect taxa. These results are opposite those predicted by the plant stress hypothesis (plant stress should promote outbreaks of phytophagous insects).
6. The bottom-up effects of plant nutrition and vegetation structure mediate the strength of top-down impacts on phytophagous insect populations. Predators are only able to exert significant suppressive effects on herbivore populations in habitats with low-quality host plants and complex vegetation structure where herbivores develop slowly and predators aggregate.

7. Robert Denno was an internationally respected figure in population and community ecology, known for his cutting-edge empirical studies and his penchant for synthesis. However, his lasting impact on the field of insect ecology is primarily as a devoted mentor who produced an extensive academic lineage of students and postdoctoral associates.

DISCLOSURE STATEMENT

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