THE INFLUENCE OF LARVAL ECOLOGY ON OVIPOSITION AND MATING STRATEGIES IN DRAGONFLIES

RUTH E. BUSKIRK AND KAREN J. SHERMAN*

SYNOPSIS

Reproductive behavior of adult dragonflies can be related to ecological requirements of their aquatic larvae. Based on the literature on larval ecology, we suggest patterns of female oviposition behavior that should place offspring in favorable situations, appropriate for the species. The predicted patterns, with respect to microhabitat use and spatial distribution of eggs, largely agree with our observations of oviposition behavior in seven species of pond dragonflies. By knowing the behavior of ovipositing females, we can predict the most feasible strategies for male dragonflies to maximize their breeding success. Whether males employ territorial defense and whether they guard their mates following copulation is related to the manner of oviposition of the female in sixteen species of dragonflies surveyed. In order to test these predictions further, we call for more detailed observations of female oviposition behavior and other features of adult mating systems that are directly related to survival of young offspring.

Dragonflies spend most of their life cycle as aquatic larvae or nymphs (Corbet 1962, Paulson and Jenner 1971), and pond and lake studies indicate there is up to 99.9% mortality during these aquatic stages (Benke and Benke 1975). In dragonflies of the temperate zone, individuals are in the adult stage only a few weeks, a small fraction of their total lifetime. Following emergence as adults, females produce batches of mature eggs, mate, select appropriate oviposition sites and deposit their eggs. Eggs may be dipped or flicked into water or mud, or they may be inserted into vegetation with the female’s piercing ovipositor (Corbet 1962, 1969, Paulson 1969). Males patrol the oviposition habitats, may defend areas against other males, and attempt to mate with any solitary female they see.

In recent years odonates have been the subject of several excellent behavioral ecology studies in which mating systems were investigated with a consideration of individual strategies and variability within a species (Alcock 1979, 1982, Campanella 1975, Campanella and Wolf 1974, Fincke 1982, Pezalla 1979, Sherman 1983b, Ubukata 1975, Ueda 1979, Waage 1979, Wolf and Waltz 1984). Research has concentrated primarily on the adult males and, from observations of individually marked animals, how their successful strategies vary with age, population density, and resource configuration. For example, at an earlier symposium in this series, Waage (1983) calculated the costs and benefits of various territoriality strategies in males of Calopteryx damselflies.

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The objective of this paper is to draw attention back to the selection pressures acting on the dragonfly egg and early nymphal instars. We wish to focus on features of adult mating systems that are more directly related to survival of young offspring. In particular, we are concerned with where and how the female deposits her eggs. Our approach is to consider selective pressures on the eggs and young nymphs in order to predict the optimum oviposition behavior of the female and then the related behavior of the male.

Female dragonflies have limited ability to influence the survival of offspring after egg deposition since no parental care is provided. However, there should be strong selection pressure to choose oviposition sites in which nymph survival is high. Such sites should be characterized by physical conditions that are favorable for development (temperature, oxygen concentration, water movement), that provide sufficient food for nymphs, that minimize predation and that minimize intra- and interspecific nymphal competition. Females must use general habitat cues to evaluate oviposition site quality since they are unable to use more direct assessments such as predator density or relative food supply. Females do not inspect all areas of a pond, particularly if it is large, before beginning to oviposit. Thus, they are not necessarily selecting the best oviposition sites, but initially are probably choosing adequate sites.

**Relation of Oviposition Patterns to Larval Requirements**

Several aspects of female oviposition behavior would affect survival of eggs and young nymphs, including temporal patterns, microhabitat choice, and spatial dispersal (i.e., clumping) of eggs. In addition, the behavior of females would be affected by the two primary causes of interrupted oviposition, i.e., predation on the female and disturbance by conspecific males. Temporal aspects of oviposition primarily involve selective forces on the adult female. For instance, the rate of egg release is temperature dependent (McVey 1984) and thus varies with time of day. Male activity periods affect the probability that oviposition will be interrupted by males. Male distribution, therefore, is related to the time of day females can deposit most eggs. These temporal aspects affect the larvae only indirectly, in that rapid oviposition rates at one site might lead to overcrowding in the nymphs. Because we are interested in oviposition patterns that affect success of eggs and early nymphal instars, this discussion will concentrate on microhabitat and spatial aspects, rather than temporal patterns.

**Microhabitat Selection**

Females should place eggs into habitats that are most suitable for egg and early nymph survival. Because late instar nymphs are more mobile and probably select their own microhabitats (Corbet 1982), female behavior probably has less direct impact on survival in these stages. Merritt and Cummins (1978) have classified odonate nymph habits into three broad categories: burrowers, sprawlers and climbers. Burrowers (primarily members of the families Petaluridae, Cordulegastridae and Gomphidae) live in burrows in the sediments of streams, ponds and lakes. Sprawlers (most Libellulidae, some Corduliiidae) inhabit the surface of sediments, debris and vegetation while climbers (Aeshnidae, Celithemis, Epicordulia, Leucorrhina)
move vertically on stem surfaces. However, within each category there may be considerable differences in the activity pattern of different species (Corbet 1962, Kime 1974). Johnson and Crowley (1980) suggested that nymphs can be functionally classified into two groups: cryptic “sit and wait” nymphs and actively searching nymphs. More active nymphs should be found in vegetated habitats which offer greater protection from visual predators while “sit and wait” nymphs should be found in more open habitats. Thus, females of species that have active nymphs should prefer vegetated habitats for oviposition.

The two most common sources of mortality for eggs and nymphs are predation and desiccation. Oviposition in emergent vegetation in littoral habitats would offer more protection to eggs and young larvae from visual fish predators. These heavily vegetated areas in shallow water, however, are more likely to dry up before the completion of larval development. Oviposition in open water at the center of a pond would reduce the chances of desiccation. The balance point between these two selective factors varies from species to species. For example, in dragonflies with potentially rapid growth rates, the larvae have a greater probability of maturing before the habitat dries up. In addition, the warmer water temperatures of shallow, vegetated areas or small pools would facilitate rapid growth. These groups would be expected to select small pools or pond margins for oviposition.

**Spatial Distribution of Eggs**

The consequences of spatial patterns of egg deposition in salamanders were studied by Wilbur (1977). He calculated that when there was a constant probability of egg loss to predators, then the expected number of surviving offspring would be a function of the total eggs produced, not a consequence of their distribution among different nests. He determined, however, that the mathematical variance in the number of surviving offspring increased with higher numbers of eggs per nest. Individual females with a few nests each containing many eggs would have lower reproductive success when an entire nest was lost to predation than females with more nests and fewer eggs per nest. There can be, therefore, an advantage to reducing the number of eggs deposited per single nest, as long as the cost of making new nests is not high.

These calculations also apply to dragonflies. They too have a complex life cycle and a balance between use of temporary and permanent ponds that is determined by the species’ vulnerability to predation and desiccation (Wilbur 1980). For dragonfly females the cost of “making multiple nests” would lie in finding or traveling to another pond or in movement to another site in the same pond. Females in populations with high rates of predation on eggs should have been selected to divide their egg mass by depositing smaller batches in each of several suitable locations. Species in which eggs are less subject to predation, and in which adult females are not heavily predated during oviposition, are predicted to deposit more of their egg mass at a single point within a pond.

**Predicted and Observed Oviposition Patterns for Pond Dragonflies**

From the selection pressures just discussed emerge predictable models
of adult dragonfly behavior. In this section we first present the array of oviposition patterns "available" to females, defined in terms of microhabitat and spatial distribution, and predict specific patterns for various larval requirements. We then test the predictions with observations on several species of pond dragonflies. No detailed comparative studies on the behavior of individual females have been reported previously, nor are there many experimental studies of nymphal ecology. Detailed investigations of nymphal mortality, its causes, and the location of an individual female's oviposition bouts would be needed to test these predictions rigorously. Therefore, we must rely on a few published studies of larval ecology to make predictions, and we present new observations on female behavior along with some previously reported work (Table 1).

Some of the oviposition options available to females, depending upon pond size and density of vegetation, are sketched in Figure 1. The simplest strategy would be for a mated female to select a suitable patch of habitat and deposit her entire batch of fertilized eggs as quickly as possible (see A, Fig. 1). In order to avoid having all her eggs devoured immediately by fish attracted to the oviposition movements, the female could oviposit briefly at several sites within the pond (see option B, Figure 1). Placing eggs in small bodies of water, where fish are less likely to occur, or at heavily vegetated sites, where nymphs would be less visible, could reduce fish predation on the larvae (C). When nymphal overcrowding and intraspecific competition are probable, more offspring would thrive if eggs were spread out over the suitable habitat (D). To avoid desiccation, the female could choose larger bodies of water or more open water (E), but if rapid larval development were possible, growth would be faster in smaller pools or shallower areas with warmer water (F). Females of species with more active, climbing larvae are expected to oviposit near or on aquatic vegetation (G), while species with nymphs that are sprawlers, "sit and wait" predators, may oviposit in more open water (H).

From observations of oviposition behavior we can test the predictions in several species. The widespread libellulid *Pantala hymenea* is a strongly flying species and is extremely opportunistic in selecting oviposition sites. In warm conditions larval development for this species is most rapid (Corbet 1962), and the generalist feeding, active sprawlers are apparently not often food-limited (Heyer et al. 1975). We would predict pattern F (small bodies of water) and, especially in variable habitats, a reduction of reproductive variance by distributing a single batch of eggs among many sites. In fact, mated females of *P. hymenea* oviposit briefly in small pools of water and fly in tandem to many oviposition sites. The male releases his mate momentarily for her to dip her abdomen one to fifteen times in small bodies of water, that range from water-filled footprints to swimming pools.

In Table 1 larval susceptibility to predation is inferred from the consistent breeding failure of *Anax junius* and *Plathemis lydia* in study ponds with fish (Johnson and Crowley 1980). Vulnerability to predators was also demonstrated by the extreme increase in dominance of *Pachydiplax longipennis* in fish exclusion experiments by Morin (1984), while lack of predation pressure on larvae was suggested for *Perithemis tenera* in the same experiments. In the three species in Table 1 considered most vulnerable to fish predation, the females oviposit only in heavily vegetated areas; in fact,
<table>
<thead>
<tr>
<th>Species</th>
<th>Larval Ecology and Reference</th>
<th>Predicted Oviposition Pattern$^1$</th>
<th>Observed Oviposition Pattern$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Anax junius</em></td>
<td>active climbers (Corbet 1962)</td>
<td>G, C</td>
<td>C many eggs per site</td>
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<tr>
<td></td>
<td>not food limited (Folsom and Collins 1982)</td>
<td></td>
<td>few sites, widely dispersed</td>
</tr>
<tr>
<td></td>
<td>susceptible to fish predation (Johnson and Crowley 1980)</td>
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<td></td>
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<tr>
<td><em>Ladona deplanata</em></td>
<td>synchronous larval development (Benke and Benke 1975)</td>
<td>D</td>
<td>D few eggs per site</td>
</tr>
<tr>
<td></td>
<td>larval competition among odonates (Benke et al. 1982)</td>
<td></td>
<td>few meters between sites</td>
</tr>
<tr>
<td><em>Libellula luctuosa</em></td>
<td>sprawlers in mud (Corbet 1962)</td>
<td>H</td>
<td>B, H variable eggs per site</td>
</tr>
<tr>
<td><em>Pachydiplax longipennis</em></td>
<td>vulnerable to fish predation</td>
<td>C</td>
<td>C variable eggs</td>
</tr>
<tr>
<td><em>Pantala hymenea</em></td>
<td>rapid development (Corbet 1962)</td>
<td>F</td>
<td>F few eggs per site</td>
</tr>
<tr>
<td></td>
<td>not food limited (Heyer et al. 1975)</td>
<td></td>
<td>many dispersed sites</td>
</tr>
<tr>
<td><em>Perithemis tenera</em></td>
<td>active crawlers (Needham and Westfall 1955)</td>
<td>G</td>
<td>A, G many eggs per site</td>
</tr>
<tr>
<td></td>
<td>not predation limited (Morin 1984)</td>
<td></td>
<td>single site</td>
</tr>
<tr>
<td><em>Platthemis lydia</em></td>
<td>vulnerable to fish predation (Johnson and Crowley 1980)</td>
<td>C</td>
<td>G many eggs per site</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>few close sites</td>
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$^1$See Figure 1.

$^2$Observations by authors (localities and supplemental data sources same as in Figure 2).
Fig. 1. Schematic diagrams of possible oviposition patterns, with respect to pond size, density of vegetation, and spatial distribution of eggs for pond dragonflies. Individual options B through H would be predicted for species with the different larval requirements indicated.

females of *A. junius* oviposit endophytically, usually in tandem position with their mates. Spring emergence species such as *Ladona deplanata* have more synchronous larval development than other dragonflies (Benke and Benke 1975, Benke et al. 1982). As predicted in such species with potentially more larval competition (pattern D), the female of *L. deplanata* moves erratically around the perimeter of the pond as she oviposits. Nymphs of *Libellula* species are sprawlers, and the female tends to oviposit in more open water and more widespread sites, often wandering outside the comparatively large territory held by her mate.

As many of the examples in Table 1 indicate, there is agreement between the observed oviposition behavior of pond dragonflies and the basic larval requirements. A good deal of variability exists among and even within females in a species (e.g., Paulson 1969, Sakagami et al. 1974, Sherman 1983a). With more intensive observations of marked individuals in the future no doubt even more variability will be documented. We may find that individual behavior patterns are a mixture of distinct stable strategies (Broekman 1980) or perhaps a set of conditional strategies (Cade 1980). In general, the existing information on larval ecology suggests a relationship to the oviposition pattern of adult females of the species.
A broad spectrum of male behavior, with considerable variability within a species has been described for odonates (Alcock 1979, 1982, Corbet 1962, 1980, Jacobs 1955, Moore 1952, Panjunen 1966, Parr 1983, Pezalla 1979, Ueda 1979, Waage 1983, Wolf and Waltz 1984). Much of the variability in pond dragonfly behavior lies in two characteristics: the extent to which males occupy or defend specific sites and the extent to which males defend their mates following copulation. Just as in many other animals (Emlen and Oring 1977, Thornhill and Alcock 1983), the probable selective pressures on odonates are elucidated when the occurrence of females is considered a type of resource and male behavior viewed as a resource-based strategy (Campanella 1971b, Sherman 1983a, b).

If the distribution of reproductive females is predictable in space and time, males that defend a preferred oviposition site can be expected to have an advantage over males that do not. Males that have more oviposition sites in their defended areas tend to obtain more matings. Frequently, males vigorously defend small areas where females visit the pond at specific times of the day, for example, Plathemis lydia (Campanella and Wolf 1974), Perithemis tenera (Jacobs 1955), and Erythrodiplax funerea (Buskirk, personal observations). The number of matings obtained by territorial males also depends upon the density of males at the pond (Panjunen 1966, Campanella and Wolf 1974, Parr 1983, Sherman 1983a, Wolf and Waltz 1984). At very low densities, males flying over larger areas to seek females may be more successful than localized or territorial males. At very high male densities, the proportion of time that a male spends in flight increases (Fried and May 1983), and territorial males could spend so much energy in fighting that they would obtain no matings.

Detailed observations on several species indicate that the temporal and spatial distribution of females is related to the pattern of pond use by males (Campanella and Wolf 1974, Pezalla 1979, Sherman 1983a). Comparisons of the mating systems of many species show the same relationship. In Figure 2 sixteen species of pond dragonflies are categorized behaviorally, on the basis of our observations supplemented with some data from the literature. Female oviposition (spatial distribution of eggs) for each species is placed on a scale from “scattered” (few abdomen dips at each site, many widespread sites) to “clustered” (entire clutch deposited at one site). Highly clustered oviposition is exemplified by a Perithemis tenera female that, following copulation, dipped continuously in one 15-cm opening of water in an algal raft for 165 seconds then left the pond. On the other extreme a Pantala hymenaea female dipped her abdomen no more than 12 times, usually 1-4 times, in emergent vegetation and moved a few meters between each oviposition bout. In Figure 2, circles indicate species with males that display site-specific territorial defense. Note that all species in which females have highly clustered oviposition patterns show some territoriality. Species in which oviposition is spatially scattered tend not to show site-specific defense by males.

The second aspect of male behavior, the extent to which males defend their mates following copulation, is also related to female oviposition patterns in Figure 2, For several species of odonates (Alcock 1979, 1982, Sherman 1983, Waage 1979, 1983) it has been shown that when a male de-
Fig. 2. Relationship between female oviposition behavior and male behavior for pond dragonflies. Oviposition pattern ranges from scattered (few abdominal dips at each of many distant sites) to clustered (many abdominal dips at a single site). Male defense of his mate following copulation can range from none to hover-guarding to tandem, contact guarding. Species observed by the authors (localities: CR—Costa Rica, MN—Minnesota, SC—South Carolina, TX—Texas) are: A—Aeschna canadensis (MN, also Whitehouse 1941), B—Anax junius (SC, TX), C—Anax longipes (SC), D—Erythemis simplicicollis (SC, TX), E—Erythrodiplax funerea (CR), F—Ladona deplanata (SC), G—Leptethis vesiculosa (CR), H—Libellula auripennis (SC), I—Libellula croceipennis (TX, also Williams 1976), J—Libellula luctuosa (TX, also Campanella 1975, Pezalla 1979), K—Pachydiplos longipennis (SC, TX), L—Pantala flavescens (TX, also Sakagami et al. 1974), M—Pantala hymenea (CR, TX), N—Perithemis tenera (TX, also Jacobs 1955), O—Plathemis lydia (TX, also Jacobs 1955, Campanella and Wolf 1974), P—Tramea carolina (SC). Circles indicate species in which males show site defense.

If the female after mating, she deposits more eggs (presumably fertilized by his sperm) than when there is no defense. This male behavior may take the form of non-contact guarding in which the male hovers above the ovipositing female and vigorously chases away other odonates that come near, or contact guarding when the male joins in tandem flight with the female and they move together to oviposition sites. Note in Figure 2 that
most species with clustered oviposition sites for individual females tend to involve non-contact, hover-guarding by the males. For those species in which females show more widely dispersed oviposition, the data suggest that two possible strategies may be followed. In some species (e.g., *Pantala, Tramea*) males utilize contact guarding and defend their mates in the tandem position. On the other hand, it appears that in some circumstances (Fig. 2: *A. Aeshna canadensis; G, Lepthemis vesiculosa*) males abandon mate guarding entirely, when female oviposition is widely scattered and far from the copulation site. This strategy appears to characterize a number of stream dragonflies, such as some gomphids and cordulegasterids, as well.

A limitation of the conclusions from Figure 2 is that the data points are oversimplified for many species. In a study of the libellulid *Sympetrum parvulum*, Ueda (1979) found that territorial males hover-guard over their mates, but in wandering males the incidence of tandem mate-guarding increased as population density increased. Variability in contact guarding with male density also appears in *Pantala flavescens* and *Tramea carolina* (authors’ observations). For several species in Figure 2, then, population density and momentary sex ratios at the pond can affect the extent of male territoriality, mate guarding and female movement. Despite variability within species, however, the major correlations between male and female behavior patterns remain clear.

An additional complication is that male behavior has a short-term direct effect on female oviposition behavior. Females of species that tend to lay many eggs at one point in the pond when undisturbed or when guarded show a more widely dispersed pattern if disturbed regularly by conspecific males. On the other hand, observations on some species suggest that the hovering male may “herd” the female and induce her to stay longer in his territory (e.g., Campanella and Wolf 1974). A male, however, can rarely confine a female to his territory. Behavioral interactions between the sexes contribute to the variability seen in oviposition patterns.

**DISCUSSION**

From this brief survey we speculate that the mating behavior of adult dragonflies can indeed be related to ecological requirements of the aquatic egg and larval stages. The spatial configuration and microhabitat use of ovipositing females can be predicted from knowledge of larval ecology (Figure 3). The extent of territoriality and mate-guarding behavior in males of a species is related to the oviposition pattern of the females. Natural selection favors male behavioral strategies that provide maximum oviposition by their mates in suitable habitats. Territorial defense by males is only advantageous when females are predictable in time or space.

The major selective factors on adult dragonfly behavior are shown as solid arrows in Figure 3. Larval ecology for each species determines which female oviposition pattern(s) will convey most reproductive success. Microhabitat selection by ovipositing females should place eggs in locations that are appropriate for the habits and behavior of the nymphs. Males seek mates at the oviposition habitat. Territorial decisions by males at the pond should be made on the basis of female predictability in space and time and of male population density. Whether a male employs territorial defense or guards his mate following copulation depends upon the movement patterns.
of the ovipositing female. There is variability within a species, and often within an individual, for components of the model in Figure 3, with the greatest variability in male behavior. Previous studies of marked individual dragonflies indicate that there are extreme differences in reproductive success (number of matings) among males in a population (e.g., Sherman 1983a, Wulf and Waltz 1984).

Short-term factors affecting reproductive behavior, including population parameters and habitat variables, are depicted as open arrows in Figure 3. These variables affect mating behavior, but in this scheme they are only ancillary evolutionary factors. Behavior of the adults is ultimately shaped by the ecological needs of eggs and young larvae.

In addition to behavioral studies of individual male odonates, therefore, we call for closer study of the relationships between adult mating systems and selective pressures on the eggs and young nymphs. A detailed look at female oviposition behavior can provide the framework necessary to link these different aspects of reproductive success. Previous observations of oviposition microhabitat can be combined with new studies of the movements of marked females.

There is a practical use that can be made of such information. Larval odonates have been used for monitoring environmental quality (Carle 1979, Voshell and Simmons 1978), and in some stream species with narrow habitat requirements, a shift in adult species composition can be seen in association with relatively small changes in water flow and vegetation structure. Adult shifts thus can also serve as indicators of water quality. Because of the great variability in male behavior, there is actually more information available from observations of female oviposition.

The information on presence of adults, however, must be used with discretion. For example, in a survey in Australia (Watson et al. 1982), odonates of all life stages decreased in abundance immediately downstream from a source of sewage effluent, and though the adult fauna recovered further downstream, larvae of some species remained absent. Thus, population analyses based on adult stages only, particularly adult males, will not necessarily provide information on long-term effects of environmental change.
on odonates. Note that locality records of adult male odonates of an endangered species (e.g., Bick 1983) may not provide confirmation that the species is breeding successfully at that site. Perhaps as we learn more about larval requirements, as well as the associated oviposition patterns and male behavior, it may be possible to monitor habitat change using observations of the adults of certain indicator species.

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