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BIOLOGY OF ODONATA

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INTRODUCTION

Odonata, or dragonflies, constitute a small, well known, widely distributed order of insects. The 5000 or so species belong to three suborders (all referred to here as dragonflies): the Anisozygoptera, containing only two known species; the Zygoptera; and the Anisoptera. Typically large and active by day, the winged adults are conspicuous at ponds and rivers, which usually form the encounter site (see 155) or "rendezvous" (30) where reproductive behavior takes place. Accordingly, dragonflies provide valuable models for interpreting the behavioral interactions of many other insects that assemble for mating but are less readily watched in the field.

Two books treat the biology of the order: the first (201) emphasizes systematics and functional morphology, and the second (30), ecology and behavior. This article is a review of the main features of the dragonfly life history and so can be regarded as a highly condensed supplement to the second of these books. Accordingly, I give prominence here to research published after 1960, and have not cited sources for information already reported in the second book (30).

A topic not reviewed but which deserves mention here is the growing extent to which faunistic records are being used as source material by scientists who are trying to check or mitigate habitat destruction and species extinction by recommending the creation of nature reserves (e.g. 4, 136, 186, 225). As freshwater insects, dragonflies are exceptionally vulnerable to urban and agricultural expansion, which commonly entail the draining of ponds and marshes.

HABITAT SELECTION

Immediately after emergence, adults typically fly away from water, not returning until reproductively mature, several or many days later. At this

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time, some species "home" precisely to the pond from which they emerged (212), but such behavior is probably exceptional. Dispersal during the maturation period is often sufficiently extensive (e.g. 146) that mature adults will need to respond appropriately to cues when seeking a rendezvous.

Cues employed during habitat selection can be inferred from the microgeographic distribution of adults and from the microhabitat requirements of larvae. Ponds lacking Odonata tend to be temporary, shaded by trees, and to have little aquatic vegetation (50, 51). Removal of trees can promptly change the species spectrum (39); and both the kind and distribution of aquatic plants (sometimes since they serve as oviposition sites) may also affect the numbers and spacing of larvae which live among them (94, 117, 190). Likewise, cues can be inferred when man-made habitats are colonized. *Bradinopyga geminata,* which probably is a normal inhabitant of rockpools, now commonly oviposits in cement tanks in India (98). A newly formed dam is occupied first by species with a wide microgeographic distribution, and then by those characteristic of later stages of ecological succession (6, 216).

OVIPOSITION

Females either lay eggs "endophytically" within or among plant tissue or similar material, or "exophytically" by releasing them above or upon a surface. Egg-laying behavior can be classified from a functional (44, 185) or phylogenetic (63, 163) perspective; but much variability exists among species and (within species) among populations (167) and even among individuals (163) so that it can be difficult to distinguish exceptional from typical behavior (10). Recent findings are considered in relation to two reference points: the endophytic and exophytic dichotomy; and site selection, especially as this relates to the prospective environment of the egg and newly hatched larva.

Endophytic dragonflies normally place eggs inside plants, and usually in living tissue, although certain tropical Gynacanthinae oviposit in moist mud (42). When choosing plants, species may be catholic (e.g. 15, 34) or, more commonly, selective (e.g. 115), a phenomenon that may be studied using simulated oviposition sites (220). Exophytic species show special modifications when eggs are positioned within a habitat. The female of the stream-dwelling *Belonia croceipennis* uses the tip of her abdomen like a ladle to scoop up drops of water and flick them, with the eggs, onto the bank (230). She thus wets the eggs (which probably makes them sticky) and at the same time positions them above the water level. Certain riverine gomphids lay eggs equipped with grappling devices (3, 33) that become functional upon contact with water. In seasonal ponds and swamps, species of *Micrathyria* exhibit several kinds of behavior: they may drop the egg from above onto the water, release the egg while tapping the water or a leaf with the abdomen, or place the egg on or beneath a leaf or on mud (163).

The choice of oviposition site plays a role in winter survival and seasonal regulation of three Lestidae which coexist in ponds in the Canadian prairies. All overwinter only in the egg stage, and all oviposit in *Scirpus* above the prevailing water level; but the species differ in ways that correlate with the developmental requirements of the egg. *Lestes disjunctus* and *L. unguiculatus* oviposit only in green stems, preferring those growing in small groups or bordering large stands. The female seals each incision after inserting an egg. The thin-walled egg, which is susceptible to desiccation and which needs exogenous moisture to complete prediapause development, does so by the end of August before the stems die. Stems chosen are the first to collapse in late-autumn storms and as a result become snow covered and insulated against cold relatively early (180). *Lestes congener* begins to oviposit later and, in contrast, only in dry stems, preferring those that are bent or broken and towards the center of stands. The incision is not sealed. The thick-walled, relatively cold-resistant egg undergoes little embryogenesis in autumn but enters diapause in winter before completing katatrepsis (movement of the embryo from the ventral to the dorsal surface of the egg). The choice of broken stems ensures wetting in early spring, a prerequisite for embryogenesis to continue (179).

Ovaries of Odonata are of the panoistic type (3, 197), and eggs are laid in successive episodes, often within the same day. In the Zygoptera studied, about 100–400 eggs are laid per episode (15, 79, 220); individual *Calopteryx maculata* can lay 525–750 eggs per day and 1267–1810 over a period of 4–14 days (220). Anisoptera usually lay several hundred and sometimes several thousand eggs per episode (18, 30, 131).

THE EGG STAGE

Duration of the egg stage depends primarily on whether it is the overwintering stage. Eggs of many tropical and temperate species exhibit direct development and hatch after 5–40 days, whereas those of certain other temperate species, notably of *Aeshna, Sympetrum,* and *Lestes,* undergo delayed development, overwinter, and hatch after about 80–230 days (3).

Among eggs that overwinter, two main types exist: those laid in summer, which complete katatrepsis in autumn and then overwinter as full-grown embryos; and those laid in late summer and in autumn, which overwinter before completing katatrepsis (3). Most species of *Lestes* (178) and *Sympetrum* (3, 18, 194), and certain *Aeshna* fall in the first type; *Lestes congener*

(178) and most species of *Aeshna* (3) fall in the second. Sometimes, perhaps when the oviposition period is protracted, both types may be found within the same population of one species (18). The rate of development and the time of hatching of overwintering eggs are regulated seasonally by the existence of three phases of development (termed prediapause, diapause, and postdiapause development), each characterized by a distinctive response to temperature (18). Such responses may be augmented, as in some *Lestes* (178), by a sensitivity to photoperiod, which apparently reduces the frequency of the deviant hatching that occasionally occurs in autumn (51). Prolongation of the adult prereproductive period in warmer parts of a species' range (e.g. 18, 38, 189, 212) and the terrestrial oviposition shown by many species of *Sympetrum* (e.g. 194) may have the same effect (see 210).

Eggs laid by a single female on the same day can vary widely in the date of hatching. In *Aeshna cyanea* and *A. mixta,* egg duration is correlated positively with the proportion of larvae exhibiting different rates of growth and different numbers of instars in captivity (182, 183), although the ecological implications, if any, of this relationship remain unknown. Such a correlation is not shown by *Somatochlora viridiaena,* which displays a bimodal temporal pattern of egg hatching; larvae from a single egg batch may take one or two years to complete development in captivity (132).

THE LARVAL STAGE

Generally, larvae occupy conventional aquatic habitats. However, certain sylvan Zygoptera develop in the water that accumulates in the leaf bases of plants (e.g. 120), and a megapodagrionid, *Podopteryx selysi,* occupies water-containing tree holes (226), which may perhaps prove to be the habitat also of a supposedly terrestrial larva collected from leaf litter in New Caledonia (see 109). The larva of the aeshnid, *Antipodophlebia asthenes,* which inhabits subtropical rain forest in Australia, is probably terrestrial, at least in later instars (J. A. L. Watson, personal communication, 1979). Larvae of a few species can survive out of water for up to a month or so (50, 196, 228), but in the typical life history this is rare.

Site selection within the aquatic habitat has implications for resource partitioning and for concealment from both predators and prey. Certain burrowing larvae locate themselves according to substrate particle size (91, 174), probably by using tarsal sensoreceptors (91). Apparently such site selection is related functionally to both the mechanics of digging (174) and the need to avoid obstructing the anal respiratory orifice (91, 174), a requirement supposedly correlated with extreme hyperdevelopment of the tenth abdominal segment in some gomphids (e.g. 33).

Feeding

Odonata larvae are generalized predators that detect their prey by means of their compound eyes and/or mechanoreceptors (171, 172). The prey is caught by sudden extension of the labium (21, 173) or, when large larvae catch small prey, merely by movements of the labial palpi (105). Eye specialization and larval feeding mode are closely related (187), and an orderly ontogenetic change occurs in the responses and sequence of actions involved in prey capture (see 22). Feeding behavior [which may include the killing but not the consumption of prey (82)] is influenced by factors such as the degree of hunger (48, 69, 82, 123), the time that has elapsed since the last molt (82), and the density (82, 199), size, and movement (22, 69, 105) of potential prey. Food in nature varies according to the position of the larva in the aquatic habitat, the type of labium (169), the season (25), and the size and relative availability of prey species. As larvae grow, individual prey items become larger (46, 200) and more varied (104), mainly because larger larvae retain the ability to consume small prey (46, 58, 105, 117, 200). Cannibalism among Odonata larvae in nature is very rare (see 8, 105).

Feeding rates are lower in Odonata than in herbivores of similar size (153). In the relatively inactive, semivoltine *Pyrrhosoma nymphula,* which, like *Ischnura elegans* (200), derives much of its food energy from chironomid larvae (105), the actual feeding rate depends on the size of the dragonfly larva, water temperature, season, and the imminence of metamorphosis, and varies between 20 and 70% of the estimated maximum feeding rate (106). In *I. elegans* the onset and termination of seasonal growth occur at the temperature at which the attack coefficient begins to increase markedly (199).

Larvae usually remain on one perch (176) or in the same burrow (196) or leaf base (120) for long periods, but they may also wander, especially if hungry (94), and especially at night (80, 174, 229) when they also feed (199). The number and distribution of vantage points for feeding, provided naturally by certain rooted aquatic plants, are thought to influence the numbers and rate of growth of larvae of some Zygoptera (117). The existence of territorial behavior among larvae, anticipated by Macan (119) and Machado (120) and demonstrated by Rowe (176), may help to regulate population density. Future understanding of intra- and interspecific competition in Odonata will be helped by the knowledge that age cohorts within a species tend to be spatially separated [perhaps partly as a result of size-dependent preferences for different perch diameters (94)] and that larvae of the same age cohort show seasonal movements within a body of water (74, 94, 118).

Production

As is usual in carnivores, the food-energy assimilation efficiency of Odonata larvae is high—almost 90% in each of four species studied (105, 122, 153). In *Pyrrhosoma nymphula* assimilation efficiency is influenced by prey type and larval size, but is virtually independent of feeding rate, temperature, and developmental condition with regard to diapause or metamorphosis (105, 106). Fischer's finding that assimilation efficiency increases with larval size in *Lestes sponsa* (52) has not yet been reconciled with Lawton's demonstration of the inverse relationship in *Pyrrohosoma nymphula* (105).

The relative inactivity of larvae means that net production efficiencies are high; and this, in combination with a high assimilation efficiency and high mortality (9, 107, 124), means also that gross population growth efficiency, maximum ecological efficiency, and production : biomass ratios can be high (8, 107). Odonata have a standing stock that is often 2–3 times greater than that of their prey and also, a large daily consumption capacity (8). In cool-temperate latitudes, production may effectively cease during winter (107), but in warm-temperate latitudes it can occur relatively evenly throughout the year (8). In the latter situation an inverted predator : prey biomass pyramid may exist, suggesting that Odonata larvae play a major role in the regulation of their prey (8). In this regard, Lawton's detection of two separate energy-utilizing pathways in a pond containing *Pyrrhosoma nymphula* (105) shows the need to refine aggregate values for prey biomass when estimating production and prey turnover.

In a large pond in southern India the outflow of energy through the emergence of five species of Anisoptera amounted to 0.00002% of the gross primary productivity of the pond; corresponding values for detritivores and herbivores are between 1 and 0.1% (124). Each year this pond gained about 73 Kcal through oviposition and lost about 620 Kcal through emergence of one of the species, *Brachythemis contaminata* (124). Although parameters such as average density, mortality rate, and the number emerging can fluctuate markedly from year to year (9, 107), population energy flow has been found to be much less variable (9, 107, 124).

Rate of Development

It is usual for species in permanent lowland habitats in tropical and warm-temperate latitudes to complete one or more generations per year, and for species in warm- to cool-temperate latitudes to be univoltine or semivoltine; but several species maintain obligatorily univoltine life cycles well north of 50°N (e.g. 179). Although the relationship is not simple, voltinism shows a regression, both interspecifically and intraspecifically, on latitude and altitude. For example, different species take as long as 4–6 years to complete a generation near the Arctic Circle (141) and 3–4 years or more in upland bogs (196) or streams (80); and in Europe populations of one species, *Ischnura elegans,* are mainly trivoltine at 43–44°N, univoltine at 53–54°N, and semivoltine at 57–58°N (74, 199). Likewise, within the same body of water some larvae take an extra year to complete development, sometimes due to low temperature (47), or perhaps to diminished food supply (117).

The simplest pattern of larval growth, in which the rate seems to be primarily a result of temperature and food availability, is found in the tropics and among some univoltine temperate species which overwinter only in the egg or adult stage. Several species of Zygoptera and Anisoptera in tropical (97, 192) and temperate (e.g. 194) climates routinely complete larval development in about two months, and a few Anisoptera inhabiting temporary pools (30) and certain Lestidae (51, 179) in a somewhat shorter period; but apparently most Anisoptera with such a simple pattern of growth complete larval development in about 100–200 days (e.g. 61, 96, 98, 191). The number of larval instars, which varies within and between species, may be from 9 to 15 (see 122).

Since the larva is the overwintering stage for most temperate species, its rate of growth does not depend solely on temperature and food. Instead, growth rate is controlled by the interaction of responses to temperature and photoperiod such that morphological development within and between certain instars is arrested or accelerated at different times of year. Such systems of regulation are functionally related to factors such as the seasonal placement of emergence, its duration, and its synchronization within the emergence period. At higher latitudes the time available for adult activity becomes less and the number of instars that precede emergence in the same year decreases. This cline can be discerned among and within species and correlates with climate as well as latitude (140, 166).

A relatively simple example of the regulated condition is provided by *Lestes eurinus* in North Carolina at about 36°N where populations overwinter in the three larval instars preceding the final one (110). Over a wide temperature range larvae of these instars (and the final one) develop more rapidly at summer than at winter photoperiods (111). Such a response magnifies the seasonal change in growth rate due to temperature and also provides a measure of compensation in spring and autumn for the seasonal lag in temperature.

More complex responses to temperature and photoperiod exist among certain other species studied in North Carolina (47, 71, 112, 113) and southern Ontario (35) in North America, and in England (30) and Sweden (140–142) in Europe. A feature common to these species is that one or more late instars become refractory (unresponsive) to long-photoperiod stimulation in late summer or early autumn and thus enter a phase of suppressed development sometimes referred to as diapause (see 112). In *Pachydiplax* *longipennis* the refractoriness declines in intensity after its inception in late August and disappears by April (47). Termination of diapause in *Enallagma hageni* and *E. aspersum* can be caused experimentally by exposure either to low temperature, regardless of photoperiod, or to short photoperiods at a permissive temperature (71).

A critical element in the seasonal regulation of many dragonflies at higher latitudes is the annual reversal of response to photoperiod that occurs among one or more late instars at, or somewhat before, the autumnal equinox. This reversal can induce the population to molt synchronously at that time and can also establish a latent sensitivity to spring photoperiods (113). For example, in *Epitheca cynosura* (in North Carolina at 36°05'N) this reversal is associated with entry to the final instar and occurs soon after the equinox (112); in *Leucorrhinia intacta* (in southern Ontario at 43°32'N) a similar reversal occurs before the equinox at the end of August (35). In the European *Leucorrhinia dubia* which, like *E. cynosura* and *L. intacta,* spends its last winter mainly in the final instar, analogous differential responses to photoperiod operate within the final instar and thus enhance the degree to which each of several developmental phases is synchronized within the larval population (142). Such responses prevent autumnal emergence and reduce temporal variation among overwintering larvae that are due to emerge in the succeeding summer. Further synchronization, perhaps of special significance for species that spend the winter before emergence in several instars, can be accomplished in spring and early summer by a system of rising lower temperature thresholds (111) among two or more instars or developmental stages within an instar (35).

EMERGENCE

The seasonal placement, duration, and synchronization of emergence within the emergence period tend to be consistent for a species in a given climatic situation (29, 101, 114, 124, 206, 207, 227), even though these parameters sometimes show considerable intraspecific variation at the same habitat in different years (102, 231) and at different habitats in the same year (156). In temperate species, it is among those emerging earliest in the year that one encounters the shortest duration of emergence and the closest synchronization (e.g. 184); and sometimes, as expected, these features correlate closely with the number of overwintering instars preceding emergence (9). It can happen that virtually the whole annual emergence is confined to one day (77), but normally the annual duration of emergence is somewhat less than one month in species having an early, closely synchronized emergence, and a month or considerably more in others. Synchronization of emergence (within the emergence period) can be close, especially in species emerging early. In three such species with emergence periods of 13–24 days, the central 90% of the population emerged within only 4–7 days (207).

In warmer situations among larger Anisoptera, emergence typically occurs at night: pharate adults leave the water soon after sunset, and the maiden flight occurs during dawn twilight (205). In colder situations, emergence is often displaced to the daytime, beginning after sunrise (e.g. 146) and lasting several hours (101, 184, 227). A single population can show nocturnal and diurnal emergence on the same or different days, depending on the ambient air temperature after sunset. In *Anax junius,* which exhibits such "divided emergence" (see 29) near the northern limit of its range, the diel pattern of emergence reflects the threshold temperature for ecdysis, which is about 12.6°C (205).

THE ADULT STAGE

The Prereproductive Period

The prereproductive, or maturation, period lies between emergence and the attainment of sexual maturity. Typically it is spent away from the rendezvous. During this period adults may disperse far or not at all, depending on such variables as the continuity of the habitat and the presence of vegetation among which immature adults can shelter (156). In a few species the maturation period serves as the aestivating stage and consistently lasts 8–9 months (97, 207) or varies in duration according to latitude. Thus in *Lestes sponsa* the maturation period lasts about 20 days at all latitudes between 40 and 58°N, but lengthens progressively south of 40°N to about 100 days near the species' southern limit at 34°N (210). This curious pattern, which may well exist in other species, probably reflects the need for postponed oviposition in regions where the egg (in which the whole population overwinters) might otherwise hatch in autumn (210). Apart from instances of this kind, most Zygoptera studied complete the maturation period in three weeks or less [range: two days to one month (30, 38, 74, 110)], and most Anisoptera in two weeks or less [range 6–45 days (146, 184)]. The maturation period is often slightly shorter in males than in females (146, 184, 207) and is prolonged by cool weather (146, 207).

During the maturation period sequential changes occur in the color of the body (2, 17, 81, 156, 184) and wings (2, 65), in gonad development (81, 127, 146), in the size and appearance of certain ectoparasites (129), and probably in the number of endocuticular growth layers [(138) but see (214)]. With the exercise of sufficient caution, such changes can be used to estimate the postemergence age of immature adults.

The Reproductive Period

The reproductive period, which normally corresponds closely with the oviposition period, begins when adults first exhibit sexual behavior. Phenological records can be made more informative if the reproductive period and the flying season are regarded as being equivalent (30); but it must be kept in mind that, exceptionally, copulation may precede oviposition readiness by several days (175). When the flying season is discrete, its duration depends on the form of the emergence curve and on adult longevity; and for this reason those graphical statements of the flying season in which the prereproductive and reproductive periods are distinguished (184, 207) are exceptionally informative.

The seasonal placement and duration of the flying season reflect the nature of the larval habitat and its suitability for continued occupancy. In permanent habitats in the humid tropics, the flying season is probably typically continuous; elsewhere in the tropics it tends to coincide with the seasonal rains (97, 192). Outside the tropics, the flying season has a characteristic position and duration such that species can be usefully classified according to the time of year when each flies (e.g. 28, 207). For a few species that maintain resident populations in both tropical and temperate latitudes, the flying season becomes shorter at higher latitudes (204). Otherwise, the flying season of a single species in temperate latitudes varies little in position or duration over a wide latitudinal range (7, 166), although it tends to be somewhat longer closer to the tropics than it is further away (162). It appears that the flying season in Zygoptera is generally longer than in Anisoptera (see 74, 166).

The size of populations of mature adults has been estimated (see 121) only at small ponds where maximum numbers range from less than 100 in some species to more than 1000 in others (30, 53, 56, 67, 146, 156, 158, 213), and where they vary much less from year to year than do the numbers emerging (135).

Having returned to the rendezvous, mature adults tend to remain there, making only short daily movements to nocturnal roosting sites (209), unless displaced by a storm (128) or by aggressive interaction among males (67). The roosting sites to which adults repair in the afternoon or evening may be less than 1 m to 200 m or so from the rendezvous (39, 60, 161, 209) and include dense bushes (62) and grasses close to the ground (60, 161).

Longevity

Most records of longevity in nature refer only to the reproductive period: tenerals can be marked, but relatively few are recaptured (11, 67, 146, 184). During the reproductive period most Zygoptera studied live on average 1–2 weeks and up to 5–8 weeks; for Anisoptera, corresponding values are 2–3 weeks and 3–6 weeks. Daily survivorship in Zygoptera can range from 0.72 in male *Argia vivida* (56) to 0.93 in male *Ischnura elegans* (160); and in the very small anisopteran *Nannophya pygmaea* it has been estimated to be 0.82 (53). In *I. elegans,* which may well be typical in this respect, survival expectation is low among teneral adults; it then rises abruptly and thereafter gradually falls (157).

If the maturation period is included, it becomes evident that (for species that neither hibernate nor aestivate as adults) the maximum life span in nature can exceed 7–9 weeks for Zygoptera and 8–10 weeks for Anisoptera. However, some species of Aeshnidae have the capacity to live longer than this, several having survived in captivity for 11–13 weeks (36, 37). Among populations of the same species, maximum longevity varies little, but average longevity of males can differ between neighbouring ponds in the same year, being inversely correlated with the size of the population and the area of the pond (160); and it can differ between years at the same pond (30, 160, 217). Parasites are thought to reduce longevity, either directly by causing physical injury, as in the cases of eugregarine Protozoa (1) or arrenurid mites (70), or indirectly by causing hyperactivity and migration (41), as in the case of trematodes.

Feeding Behavior

Although intermediate states exist, in order to analyze certain kinds of adult behavior, including feeding, it is useful to distinguish between "perchers" and "fliers": namely, species that as adults spend most of their active time on a perch from which they make short flights, and species that, when active, fly continuously.

Throughout life, adults feed only on living prey and predominantly on flying insects (170) whose movement, size, and shape elicit the appropriate responses (134). As in the larva, specialization of the adult compound eye correlates with feeding mode (188). Zygoptera often capture resting, immobile prey (e.g. 57, 192); Anisoptera do this occasionally (45) but perhaps only if they first see the prey when it is moving or in flight (192). As catholic, opportunistic predators, dragonflies seldom diminish a prey population enough to be of obvious economic value. However, Anisoptera often assemble to feed on aggregations of prey (229) and in so doing may on occasion have a detectable impact on the numbers of pest insects (192). This happens regularly in western Tanzania where about 12 species of Anisoptera probably constitute the principal biological factor affecting breeding success of the Red Locust, *Nomadacris semifasciata* (192).

The feeding performance of perchers is susceptible to quantitative study by measuring their weight on a perch. Each day during two flying seasons, adults of *Calopteryx cornelia* and *Sympetrum frequens* respectively were making about 150 and 320 feeding flights, 43 and 51% of which were successful, and were consuming about 6 and 12 mg of food, equivalent to 11 and 14% of their body weights (68).

Color Variation

Understanding of intraspecific color variation in Odonata rests on the knowledge that it can result from the interaction of three distinct processes: polychromatism (color polymorphism), aging, and temperature-induced physiological color change. Polychromatism, supposedly genetically determined, has been detected mainly among Zygoptera (see 56, 156), although reported also in Anisoptera (42). The color changes associated with maturation, which were mentioned earlier, may continue during the reproductive period in some species (229). A third source of variation is the reversible, temperature-induced, physiological color change that occurs in several families of Zygoptera in Australia (143) and the New World (126), and in two genera of Anisoptera (86, 126, 144). This kind of change, found mostly in temperate species, is believed to facilitate thermoregulation. Typically it involves a rapid change from dull purplish or gray (the dark phase) to bright blue (the blue phase) at ambient temperatures above about 15°C, and a slower reverse change below about 10°C (143). That female *Enallagma aspersum* change from blue to gray while ovipositing under water (16) suggests that they may possess a response of this kind.

Thermoregulation

The ability of dragonflies to maintain a relatively constant body temperature is related functionally to their body size and behavior, and appears to be greater in temperate than in tropical species (125). When active by day, adults possess a repertoire of actions by which they keep the body temperature less variable than the ambient temperature. Perchers and fliers, when resting, select basking sites (90, 184), resting surfaces (146), and the height of perches (125) according to ambient temperature. While migrating (at 42°N), *Anax junius* select roosting sites on the western sun-exposed sides of bushes in the late afternoon but move rapidly to the eastern sides shortly before sunrise, thus positioning themselves so that they receive direct radiation from the rising sun (31).

Perchers thermoregulate primarily by making postural adjustments which involve the body and wings, thus varying exposure of the body to the sun (125, 130). Adults of *Austrolestes annulosus,* which have the capacity for physiological color change, orient themselves, when perched or in flight, perpendicular to the direction of incident sunlight while in the dark phase and thereby raise the thoracic temperature on cloudless, windless mornings. In this way they can begin to feed two hours sooner than if they had remained perched in the shade (215). When they are cold in the early morning Zygoptera may use an array of actions, including grooming with the legs (to remove dew), wing whirring, and basking, as a prelude to normal feeding activity (145).

Among Anisoptera, some fliers are endothermic regulators in flight. They control body temperature by alternately using gliding and powered flight, and by altering the circulation between thorax and abdomen (125), which controls heat loss.

Dispersal

Since the maiden flight is oriented away from water (146), dispersal has been assumed to result from it. Probably a spectrum exists, from species that consistently "home" to the emergence site after completing the maturation period, to others such as obligate migrants that persistently fly in the same direction and thus travel far. Although it probably remains true that dispersal behavior reflects the suitability of the larval habitat for continued occupancy, recent work (41) on the migration of *Libellula quadrimaculata* shows that this relationship may not be as direct as previously supposed (30).

Spectacular migrations (i.e. mass, directional flights) of *L. quadrimaculata,* occurring at intervals of about ten years, have been reported for centuries in Europe. In 1971 Dumont & Hinnekint (41) documented one such migration in Belgium, France, and the Netherlands, and they have offered a tentative hypothesis to describe the way in which such migrations come about. Like many other Odonata, *L. quadrimaculata* is an intermediate host for trematodes which also parasitize birds. These authors suggested that two circumstances largely determine the timing and scale of migrations of *L. quadrimaculata* in Europe: first, cyclical fluctuations in intensity of trematode parasitism and thus in nervous excitation of the dragonflies by the metacercariae; and second, synchronous emergence, which, by intensifying visual interaction among tenerals, induces widespread, mass maiden flights. These flights tend to coalesce along visually prominent pathways (e.g. rivers, railway tracks) and thus attract other dragonflies en route. The operation of these factors drains large areas of dragonflies, attracts predatory birds, causes high dragonfly mortality, and enables the trematodes to reach their definitive hosts. Because they have been reduced in size, dragonfly populations remaining in the parent habitats are subsequently exposed to exceptionally intense parasitism and so are diminished still further (41).

Dispersal patterns are different where habitats are rendered unsuitable by seasonal fluctuations of moisture or temperature. In seasonal rainfall areas in the tropics, weakly flying Zygoptera (55) and certain Anisoptera (98) move to equable woodland sites during the dry season, returning to the rendezvous at the onset of the rains. Strong fliers, on the other hand, evidently follow the periodic movements of the Inter-Tropical Convergence Zone (30); they begin migration as tenerals and are carried to temporary pools where they then reproduce (192). While migrating as immature adults and perhaps later after having matured, they sometimes fly at a considerable height, descending at sunset to roost and ascending again at sunrise (31). When flying low they tend to follow visually prominent pathways (40).

In North America certain Anisoptera (e.g. *Anax junius, Pantala flavescens*) occur from the tropics to southern Canada. Mature adults are carried north by strong winds in early spring (20) and thus penetrate beyond the bioclimatic zone where larvae can survive the winter (202, 203). The progeny of such spring immigrants emerge in late summer and presumably fly south as immatures (202), accumulating in large numbers along pathways (139) and roosting in conspicuous aggregations en route (32).

REPRODUCTIVE BEHAVIOR

The Rendezvous

Although in certain species the sexes sometimes (161, 177, 181) or normally (103) meet and copulate elsewhere, for the great majority the rendezvous is at or near the oviposition site. In the typical condition mature males arrive at the rendezvous earlier in the season and in the day than females, and space themselves out before the females arrive. Males then try to copulate with arriving females. The rendezvous serves as the focus or departure point for copulation and subsequent oviposition, and therefore as the arena for sexual selection (see 155).

Territoriality

Some Odonata are properly termed territorial according to criteria recognized for other animals, especially birds (19). Thus the male of such Odonata localizes in a more or less fixed area within which he behaves in a way that evokes escape and avoidance among intruders. Among species of Odonata a gradient exists: from simple, aggressive behavior without either site attachment or residentiality, at one end, to ritualized display with site attachment and pronounced residentiality, at the other. For example, male *Onychogomphus forcipatus* become spaced out along the edges of rivulets because of fights with neighbors, but show no detectable site attachment and so move up and down the stream during the day (89). Several Zygoptera likewise show little or no site attachment (10, 12). In contrast, site attachment in *Plathemis lydia* can be very strong: males in a study population were recorded at their individual territories 91.4% of the times that they were observed at the rendezvous (24). Among species that show pronounced territoriality, a male seldom occupies a territory for more than a few consecutive days, although the most persistent individuals may remain there without interruption for 1–3 weeks (64, 65, 67, 177, 218).

For typical perchers, the territory includes a settling base from which the occupant surveys the territory, makes sallies towards intruders, and embarks on intermittent patrol flights (cruises). The proportion of residence time devoted to perching and patrolling varies within (15) and between species: *Lestes disjunctus australis* seems to maintain tenure merely by passive occupancy, remaining perched for long periods (11), whereas *Enallagma aspersum* (16) and *Ischnura verticalis* (10) spend much time cruising and when perching hardly ever do so repeatedly at one spot.

Typical fliers, principally Aeshnidae and Corduliidae, remain on the wing while at the rendezvous (90, 177, 208). In *Anax imperator* and probably certain species of *Aeshna,* an individual male will patrol the whole perimeter of a pond on some visits, but show a consistent preference for part of the perimeter on others (27). A male *Aeshna cyanea* typically patrols the whole perimeter of a pond, his progress being interrupted by short bouts of hovering; from the time that he arrives, the duration of hovering and his level of aggressiveness decline steadily, and if undisturbed he leaves after 10–40 min, returning later in the day for several sessions of temporary occupancy (90). Such a pattern, in which conspecific males partition the rendezvous temporally rather than spatially, may be usual among fliers; its existence has been detected in other aeshnids (see 27), and is suggested, though not demonstrated, by observations on certain corduliids (e.g. 208). This pattern may also have its counterpart among perchers: in individual males of *Crocothemis servilia,* flight over the territory alternates with nonterritorial perching throughout the day (49).

Aggressive Behavior

Aggressive behavior exhibited by mature males at the rendezvous is directed predominantly towards conspecific males, which consequently become spaced out in a way that is characteristic of a species and is correlated with its size (135). In species that localize, such behavior, together with the existence of topographical boundaries, determines the greatest dimension of the territory, which can range from 0.5 m or less in many Zygoptera (e.g. 10, 38, 54) and the smallest Anisoptera (211, 231) to much more than 10 m in large Anisoptera (177, 208). This dimension decreases as male density increases (e.g. 23, 24, 122), but usually stabilizes at a certain level.

The nature and intensity of aggressive behavior vary among species, and also within species according to density of males (147, 151, 152) and distance from the center of the territory (24). Simple forms of such behavior are "wing-warning" by perched males (see 10) and a display of the abdomen by males when perched (e.g. 49, 54) or in flight (e.g. 24, 208). More elaborate aggressive encounters occur in flight, progressing from mutual threat display to physical fighting (e.g. 150). In regard to the intensity of aggressive behavior that each exhibits, two kinds of mature males can exist within a population (67, 152, 211). In *Calopteryx virgo* "territorial" males show conventional territorial behavior, involving site attachment and residentiality, and are seldom displaced; "nonterritorial" males, in contrast, patrol much, fly in swarm-like groups, perch communally, and show no inter-male aggression (65, 152). A corresponding difference between "territorial" and "wandering" males exists in *Crocothemis servilia* (67) and *Sympetrum parvulum* (211). In all these species territoriality is the normal condition at low density, and the existence and proportion of nonterritorial males reflects the extent to which the number of mature males exceeds available territories. A similar, though less discontinuous, response occurs in *Leucorrhinia caudalis* and *L. rubicunda:* as density increases, individual flight areas tend to become obscured and there are fewer aggressive encounters (150, 151). These examples constitute qualifications to the concept of "highest steady density" (135) and reveal a mechanism likely to increase the proportion of males that copulate in territorial species (see 19).

The response to increasing density among fliers that patrol continuously while on the territory does not show a consistent pattern. Virtually nonlocalized at low density, the patrol flight of *Cordulia aenea amurensis* may become localized at higher density and feature defense of areas (208); but the opposite seems to be the case among *Aeshna subarctica* and *A. juncea* (184). In nonlocalized *Aeshna cyanea,* as the rate of arrival of males at the rendezvous increases, males fight more often and leave sooner; they compensate for this by visiting the rendezvous more often in a day (88). Yet another pattern of density response is shown by *Plathemis lydia:* a system of "temporal leks" develops, whereby up to five conspecific trespassers or "subordinates" may coexist in a territory as long as they show submissive behavior towards the "dominant" male (24). This system is dynamic, in that the identity of the dominant male changes from time to time, and yet is stable, in that while a male remains dominant, the frequency and intensity of his aggressive interactions with conspecific males occupying the territory are formalized and reduced.

The relationship between aggressive behavior and dispersal remains controversial (e.g. 146, 151, 158). Nevertheless Higashi (67) has demonstrated convincingly that as density increases in *Crocothemis servilia,* territorial behavior brings about the progressive, hierarchical occupancy of less attractive pools, first by territorial and then by wandering males; in this way the number of nonutilized pools decreases as population density increases.

Reproductive Isolation

Interspecific differences in the spatial (146, 195) or temporal (133, 164) properties of the rendezvous often serve to reduce the likelihood of interspecific encounters. However, the existence of such encounters (116, 135), and of hybrids (5) and heterospecific tandem pairs (43, 84, 146) shows that specific recognition is not unerring, even though recognition of species and sex is the rule. Releasers for sexual behavior by males clearly vary greatly from one species to another and include style of flight (73, 90, 149), shape and size of the abdomen (149, 161), and color of the body and wings (10, 75, 161, 219). Despite its undoubted importance for some species (221), visual recognition seems inadequate to secure reproductive isolation in others; and in these the incompatibility of male and female structures participating in either the tandem link (165, 168, 198) or copulation (224) appears to play a major part.

Recognition of the male and perhaps also of the oviposition site by the female is assisted by the precopulatory courtship display exhibited by territorial males of certain Zygoptera, notably the Calopterygidae, in which the display typically includes flights to the oviposition site and brief bouts of being transported by the water current (65, 99, 152, 219). In species which lack evident courtship, its counterpart may be the submissive posture that a male adopts when approaching a female (24). On being approached by a male, a female can indicate that she is (76) or is not (10, 26, 148) receptive; or she can try to escape by flying swiftly away (12, 13), sometimes high above the water surface (92) and often towards dense vegetation (122, 190, 208), or by dropping and clinging to the substrate below (148).

Copulation

When a male approaches a receptive female at the rendezvous, a consistent series of events follows. First, he grasps her in the tandem position—settled or in flight and with or without prior evident courtship. The pair then forms the "wheel position," and copulation ensues at the rendezvous or nearby. After copulation the male stays at or returns to the rendezvous; and, if the rendezvous is also the oviposition site, the female begins to lay eggs—either alone or with the male still in tandem or keeping station nearby (guarding).

For copulation to be effective, the male must first have transferred sperm from his ninth abdominal segment to the copulatory apparatus on his second abdominal segment (85). Except in certain Calopterygidae (76, 99), intramale sperm transfer has been observed to occur immediately after assumption of the tandem link (see 10). This behavior has also been seen to take place in certain genera of Anisoptera (10, 84, 86, 184), but in most Anisoptera it has not been witnessed, suggesting that in such cases it must occur before the male arrives at the rendezvous (148).

After the male establishes the tandem position, which usually lasts but a few seconds (122, 148), the pair adopts the wheel position. It has generally been assumed that the wheel position, in which the tip of the female's abdomen engages with the copulatory apparatus of the male, is associated solely with transfer of sperm from male to female. However, recent observations show this assumption to be incorrect. In most and perhaps all species which copulate when settled, conspicuous pumping movements, apparently initiated by the male (see 10), occur throughout the wheel position except during the brief, final phase. In *Calopteryx maculata* and probably all other species which exhibit such behavior, these movements coincide with the removal (by the penis) of sperm already in the female's spermatheca; this sperm displacement, which in *C. maculata* is 88–100% effective, is followed by insemination (222). It is consistent with this finding that in *Ischnura aurora* the wheel position (without sperm transfer) lasts 10–20 min and precedes insemination, which takes only 2 min (175).

Copulation is often interrupted (11, 12); but, allowing for this, recorded durations of copulation nevertheless appear to correlate closely with the degree of potential interference from unpaired males. Copulation is very brief (2–45 sec) in species where the pair completes copulation in flight over water (122, 131, 177), less brief (1–5 min) where the pair is settled within or just outside the rendezvous, and protracted (minutes to several hours) where it occurs far away from the rendezvous. It remains to be seen whether sperm displacement occurs also in species which habitually copulate in flight and for only a few seconds.

Postcopulatory Behavior

After copulating, the female usually begins to oviposit promptly [unless she is teneral in which case she leaves the rendezvous (175)]. In many Zygoptera and Anisoptera, the male partner remains associated with the female during oviposition. The pair may be linked in tandem continuously, or intermittently and repeatedly, as in *Tramea* (87), *Pantala* (193), *Hadrothemis* (137), and some Zygoptera that oviposit under water (12). The male (usually but not necessarily the preceding partner in copulation) may hover or perch nearby; sometimes he guides the female to the oviposition site, and then exhibits guarding behavior (e.g. 38, 59, 64, 95, 137, 220). Alternatively, the female may consistently oviposit unaccompanied by a male, as seems to be normal among species of *Ischnura* (10, 28, 157, 175). Although such variations show patterns which correlate broadly with phylogenetic affinities (see 66, 177, 218), there is wide variation within species (10, 211, 220), and even an individual pair may show a sequence during a single episode of oviposition—from ovipositing in tandem, through male guarding, to the female ovipositing alone (83). It has been supposed that the intensity of the male's association with the ovipositing female is positively correlated with the likelihood of other males interfering with her at this time. Observations by Uéda (211) support this view: females of *Sympetrum parvulum* may oviposit with a male in tandem or guarding, or alone; and postcopulatory behavior correlates with the male's aggressive status (territorial or wandering) and the density of other territorial males at the oviposition site.

Mating Frequencies

Sex-determining mechanisms in Odonata are almost always of the XO-XX type, the male being the heterogamic sex (93). At emergence the numbers of the two sexes are nearly equal, and there is usually a slight excess of males in Zygoptera (72, 108) and of females in Anisoptera (e.g. 100, 108, 124, 146, 184). It is not known at what stage in embryonic or postembryonic development these imbalances appear; nor are their causes understood (see 108).

Among adult Zygoptera it is normal for males to outnumber females at any one time at the rendezvous (11–13, 159). For example, in a population of *Argia plana* studied by the Bicks (14), 75% of individuals at water were males, and on average males were present at water on 3.6 days of a post-maturation life of 10.9 days, and females on 1.8 days of a life of 7.7 days. These disparities seem to be almost exactly compensated for by unequal frequencies of mating (11–13, 78, 159). In the same population of *Argia plana,* among adults visiting water only about half of the males mated, whereas almost all of the females did so: the average number of mating days for all recovered males and females was 0.9 and 1.6 respectively, and for those that did mate, 1.5 and 1.7 (14).

The frequency distribution of mating among individuals is likely to differ in species where males show strong territoriality and hierarchical dominance. For example, in a study of *Calopteryx maculata,* Waage (223) found that 32% of the (territorial) males observed accounted for 74% of the matings seen. Except for the Calopterygidae, in which it is known that one territorial male can copulate with several females in fairly close succession (65) and up to nine times in one day (223), almost all such species are Anisoptera. In Uéda's study of *Sympetrum parvulum,* the number of matings recorded per day averaged 1.4 and 0.5 respectively in territorial and wandering males (211). In *Plathemis lydia,* in which one dominant male and several subordinate males can occupy a territory simultaneously, mating expectancy depends on the number of subordinates present and corresponds to status. It is greatest (by definition) in "alpha" males (i.e. those that are dominant during the times of day when most receptive females visit the rendezvous), less in males dominant at other times, and least in subordinate males (24). A male *P. lydia* graduates progressively from subordinate to dominant (and sometimes alpha) status but does not hold dominant or alpha status for long on one day. This suggests that an individual has a daily energetic limit (24)—a situation that perhaps has its counterpart in the successive, brief visits to water made during a day by male *Aeshna cyanea.*

From incidental observations it is known that individual males and females of many species are capable of copulating with many different partners (e.g. 73, 223), and that a female can lay many fertile eggs over a long period without successive inseminations (30, 37).

Consequences of Behavior

Reproductive behavior in Odonata, especially when sperm displacement occurs during copulation, clearly results in strong sexual selection in favor of the male able to maintain a territory, to "take-over" (154) a female (i.e. to copulate with a female by displacing another male copulating with her or guarding her), and to remain associated with a female at the rendezvous and oviposition site. Among all species, whether or not they are territorial in the strict sense, aggressive behavior of unpaired males spaces them out along margins of the rendezvous so that they can intercept arriving females (see 13); interference with copulation and oviposition is thereby reduced and sperm competition correspondingly lessened (see 208, 218). Such behavior can also result in dispersal to untenanted habitats (67).

As territoriality becomes more pronounced, the selective advantages to a dominant male of such behavior increase because his mating expectancy rises (24).

Tandem linkage or guarding by the male during postcopulatory oviposition reduces the likelihood of take-over by other males and thus favors the sperm of the attending male. The relative benefits of tandem oviposition and guarding to the territorial male of *Sympetrum parvulum* have been incisively analyzed by Uéda (211). A male of high status (i.e. one likely to win aggressive and sexual encounters) can gain selective advantage in three ways: by being free to improve his opportunities for a sexual encounter; by taking advantage of such an opportunity; and by preventing take-over of his mate during copulation and postcopulatory oviposition. For the territorial male, the risk of take-over is small and guarding (which allows the male to be more mobile) is preferred; whereas for the nonterritorial male for whom the risk of take-over is great and the mating expectancy low, the tandem mode is preferred. An instructive variant of this situation occurs in *Calopteryx maculata,* in which territorial males frequently guard one or more nonmates, including females last inseminated by nonterritorial males. Nonterritorial males do not guard females; therefore the reproductive success of such males rests largely on the ability of their mates to exploit the guarding behavior of territorial males. It seems that the arrangement whereby a territorial male guards nonmates constitutes a nice compromise that neither enhances nor diminishes his reproductive success. Since he is guarding his own mate, the presence of nonmates does not obviously cost him extra time or energy. At the same time he is unlikely to enjoy selective advantage by trying to copulate with a nonmate for the following reasons: first, to do so would leave his own mate vulnerable to take-over; and second, his expectation of copulating successfully would be low, because, having copulated recently, both he and the nonmate would be in a condition of diminished copulatory competence. This being so, it is perhaps not surprising that the presence of guarded nonmates attracts additional females seeking oviposition sites (223).

Females of many Zygoptera oviposit under water, sometimes as a sequel to ovipositing at the surface (12). While doing so, whether or not their mates accompany them, such females gain immunity from interference (see 34). But, quite apart from this, the presence of an attendant male after copulation means that the female can lay more eggs and (considering the possibility of sperm displacement) that more of those eggs will carry genes from the attendant male than would otherwise be the case. Consistent with this is the demonstration that in *Calopteryx maculata* the mean duration of episodes of oviposition (which correlates positively with the number of eggs laid) is greatest (13.4 min) when the female is being guarded by her previous copulation partner; it is less (9.8 min) when she is being guarded by a different male, and least (2.4 min) when she is ovipositing alone (220).

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