

**TEMPORAL ISOLATION IN TWO SPECIES OF DRAGONFLIES,
EPITHECA SEPIA (GLOYD, 1933) AND *E. STELLA*
(WILLIAMSON, 1911) (ANISOPTERA: CORDULIIDAE)**

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Two Florida dragonflies of the family *Corduliidae* perform their territorial patrol flights at different times of the day. *Epitheca stella* (Wmsn.) flies during the middle part of the day, as is the case with other species of the genus, but *E. sepia* (Gloyd) is on territory from late afternoon to dusk. The two species are similar in size, appearance and structure and fly during the same season, and the temporal separation of the territorial flights may be the only reproductive isolating mechanism between them.

INTRODUCTION

One of the often-cited modes of reproductive isolation between related species is that of temporal isolation, individuals of the two species being active or breeding at different seasons or different times of day. Textbooks and ecological studies abound with examples of related species breeding at different seasons, but there is little evidence to defend the hypothesis that these differences in breeding seasons have evolved in response to direct selection for reproductive isolation. MECHAM (1961) presented a convincing argument that this has happened in certain groups of frogs, and ALEXANDER & BIGELOW (1960) discussed the very interesting situation in crickets in eastern North America. On the contrary, there are very few examples of temporal isolation on a daily basis, i.e., related species breeding at different times during the diel cycle. Thus I should like to document a case which I consider a possible example of this phenomenon.

Two species of dragonflies of the genus *Epitheca* (*Corduliidae*), *E. sepia* (Gloyd) and *E. stella* (Wmsn.), are common in peninsular Florida, USA. They are quite similar to one another in general appearance, although differ slightly in size. The wing length is about the same in the two species, but the abdomen of *sepia* (25-29 mm) is shorter than that of *stella* (32-36 mm), and in the hand this is obvious. Structurally the two are also very similar. The terminal appendages of the males differ in minor ways, including the relative length of the inferior appendage (85% of the superior appendages in *sepia* and 61% in *stella*) and the shape of the distal half of the superior appendages (becoming wider at about half their length in *sepia* and twofifth their length in *stella*). These appendages are illustrated by NEEDHAM & WESTFALL (1955), and measurements and additional descriptions of the species can be found in that publication. The appendages of the five smaller species (formerly *Tetragoneuria*; cf. WALKER, 1966) of this genus that coexist in northern Florida (*E. cynosura* [Say], *E. semiaquea* [Burm.] and *E. williamsoni* [Mtk.] in addition to the two discussed herein) are quite similar, as is the general appearance of all the species. If it were not for the varying amounts of black in the hind wings (*sepia*, *stella* and *williamsoni* have almost none, *cynosura* has more, and *semiaquea* has considerable black) and size (*semiaquea* is conspicuously smaller and *stella* and *williamsoni* have relatively longer abdomens), it would be impossible to distinguish any of these species in the field. Two that are the most difficult to distinguish are *sepia* and *stella*, and I first collected them in mixed-species swarms without realizing that two species were present. In fact, these two species were the only Anisoptera in southern Florida, among the 55 species observed over several years (PAULSON, 1966), that I usually could not distinguish in the field, and it was necessary to capture all individuals to identify them. As WESTFALL (1941) stated, the slightly shorter abdomen of *sepia* should allow recognition at close range; however, members of this genus are notorious for their rapid flight, and male dragonflies may have to make split-second "decisions" about whether to attempt mating with an approaching female before some other male does so. Thus slight differences in appearance between species might not be adequate as isolating mechanisms. In fact, my own research in progress clearly indicates they are not adequate in some species.

OBSERVATIONS AND DISCUSSION

From the specimen record, it appears that both *sepia* and *stella* are widespread and commonly occur in the same environments. Unfortunately, their larvae cannot be distinguished at present, so breeding sites can only be judged by the presence of males at the water, and I have not yet seen both species on territory at the same site. I did collect males of both on territory at a number of sites, and from these data a picture of temporal segregation has emerged. Sixteen males were collected in territorial patrol flight (cf. KORMONDY, 1959) during the day

(0900-1500) during the period 9 February to 1 April, and all of these were *stella*. Three males were collected in late afternoon: one at 1820 on 13 April, one at about the same time on 5 June, and one at 1925 on 26 July. All of these were *sepia*. The latter species is inclined to fly in late afternoon or early evening, and previous reports of it were based on specimens collected during that period. The type specimen was taken on territory at about 1800 on 7 September (GLOYD, 1933), and WESTFALL (1941) saw the species only toward evening, including one stream at which males were common just before dusk but could not be found the following morning. I did take one specimen from a feeding swarm in the morning and collected eight specimens of each species from a large swarm in midafternoon on 10 March. Thus the two species feed at the same time, but there is no evidence that they are on territory at the same time, and mating takes place while males are on territory in this genus. *E. sepia* is effectively isolated, temporally from all other species of *Epitheca* as well. I have surveyed the literature and seen all the North American species other than *E. petechialis* (Mtk.) on territory, and all the others are like *stella* in their preference for the midday period. There is no indication of temporal separation of territorial patrol flights in any other pair of coexisting species, nor have I seen this phenomenon in other genera of odonates. In some genera, in which some species are crepuscular and others more diurnal, the crepuscular and diurnal species are not particularly closely related. It may be that the evolution of crepuscularity was more likely in *E. sepia*, one of the southernmost species of *Epitheca*, but this has not happened in its congeners on the Florida peninsula, and species of *Neurocordulia*, in the same family, are crepuscular throughout eastern United States north almost to the Canadian border.

E. sepia is also different from its congeners in not having a highly synchronized emergence period and flight season. All the smaller species of the genus have quite short flight seasons in any given area, usually not exceeding 2-3 months. For example, *E. stella* flies from 3 February to 6 April in southern Florida (PAULSON, 1966); *E. cynosura* flies from 3 March to 28 April in northwest Florida (CROSS, 1956) and from 28 March to 2 May in one part of South Carolina (CROSS, 1955); the flight season of *E. williamsoni* extends from 19 April to 30 May in North Carolina (Paulson, unpubl.); and *E. semiaquea* flies from late March to 14 May in the same state (PAULSON & JENNER, 1971). *E. sepia*, however, flies from 3 March to 15 November in Florida, and I collected last instar larvae (from which adults emerged within one month) in February, March, May, June, August, and November, indicating continued emergence during that period. Probably the species is completely asynchronous, as are many odonates in peninsular Florida (PAULSON, 1966), emergence being halted only by lowered temperatures from December to February. The flight season of *sepia* has given it reproductive isolation from the other species of the genus after April in Florida, but this is presumably incidental to whatever environmental

factors have released it from the very highly synchronized pattern of the other species. It would be of great interest to determine what has caused this deviation from the common pattern.

Although KORMONDY (1959) felt that species of *Epitheca* were reproductively isolated by mechanical constraints, there is no experimental proof of this. The terminal appendages of the three Michigan species he studied were different, one of them greatly so from the other two, and this would seem to effect some mechanical isolation. However, PAJUNEN (1964) found that modifying appendages in *Leucorrhinia* (*Libellulidae*), in which the two species had appendage differences comparable to some of the species of *Epitheca*, had little effect on the successful clasping of the female and subsequent copulation. There may be a greater probability of mechanical isolation in the dull-colored corduliids with their more variable appendages than in the brightly colored libellulids with their more similar appendages (WILLIAMSON, 1906). Some of the species of *Epitheca* (*canis* [McL.], and *spinosa* [Hag.]) have very different appendages from the mode in the remainder of the species, and both of these species occur with one or more members of the group with simpler appendages. It is among the latter group that it is difficult to imagine mechanical isolation being important, and the variable size of the black spots in the hind wing may be of significance in visual isolation. This problem is being studied at present by Kenneth Tennessen at the University of Florida. In *E. sepia* and *E. stella*, both of which have almost no black on the wings, similar appendages, overlapping flight seasons, and identical distributions, the nonoverlapping times of territorial patrol flight must be very important in reproductive isolation.

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