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TEMPORAL ACTIVITY PATTERNS OF *MICRATHYRIA* IN CENTRAL AMERICA (ANISOPTERA: LIBELLULIDAE)

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Patterns of daily mating activity in 4 spp. of *Micrathyria* were determined by hourly censuses at sites in the Panama Canal Zone. *M. atra* and *M. ocellata* appear at breeding sites before sunrise and are present until late afternoon, but the time of maximum activity varies depending on the abundance of congeneric spp. and secondarily on physical factors in the environment. The smaller spp., *M. aequalis* and *Micrathyria* sp. A (nr. *eximia*) are invariably active only from mid-morning until mid-afternoon. The presence of ♀♀ at breeding sites does not always coincide with maximal ♂ activity. Less complete data are available for several other spp. in the Canal Zone and Costa Rica. — *M. atra* ♂♂ remain at breeding sites only 3-4 hrs at a time, while *M. ocellata* and *M. aequalis* individuals often are present for 8-9 hrs. Individuals of all spp. vary from day to day in timing of activity and position of local territory. Aggressive interactions are common between *Micrathyria* spp. and with several unrelated spp. The number of aggressive encounters of individual *ocellata* with *aequalis* depends strongly on the density of *aequalis* present. These 2 spp. overlap considerably in perch choice. Distribution of food within the alimentary tract of *atra* and *ocellata* suggested that they do not feed at breeding sites and that most individuals present before mid-morning have not fed since the previous day.

INTRODUCTION

The time during which an organism is active is a fundamental component of its ecology, affecting the range of physical factors to which it is exposed, the degree of competition with other organisms, the prey available to it and the predators that threaten it, and its relations with other members of the same species. Nevertheless, little quantitative information is available on the diel variation in numbers of adult Odonata present at breeding sites. Most dragonflies concentrate their activity at localized breeding areas during the middle of the day, but LUTZ & PITTMAN (1970) showed considerable interspecific variation in temporal activity patterns. Timing of activity is closely related to mating strategy (CAMPANELLA, 1975; CAMPANELLA & WOLF, 1974; PEZALLA, 1977) and is an important factor in feeding behavior (HIGASHI, 1973, 1978), but neither the principal selective forces nor the proximate factors determining diel periodicity have been characterized adequately. The numbers of breeding adults are often closely correlated with air temperature and intensity of solar radiation (HIGASHI, 1973, 1978; LUTZ & PITTMAN, 1970; NELEMANS, 1976; PEZALLA, 1977). Doubtless there is a causal relationship between such factors and activity in many cases, but difficulties exist in extrapolating from correlation to causation (MAY, 1978); other influences, especially intra- and interspecific relationships with other odonates, should be considered (MAY, 1977).

A major purpose of the present paper is to present data on the diel periodicity of several species of *Micrathyria*, and to suggest some of the reasons for variations among and within species as a whole and between individuals of different species. I hope that these data will form the basis for a more complete understanding of the ecology and behavior of this interesting genus.

MATERIAL AND METHODS

STUDY SITES

I studied quantitatively three sites in the Panama Canal Zone. The general features of two of these, Summit Gardens and Ocelot Pond, have been described previously (MAY, 1977). At Summit Gardens Ponds 1 and 2 are about 600 m^2 and comparatively open to sunlight, Pond 3 is about 300 m^2 and somewhat more shaded.

The third site is a small inlet about 1 mi. S.E. of Pedro Miguel. It empties into a larger inlet via a culvert and thence into the Panama Canal. The site had permanent water and was roughly ¼ hectare in area, with a wide band of emergent grasses and other vegetation around its margin and open water in the center; trees overhung about 20 m of the north side.

Additional observations were made at a temporary pond in a pasture at Hacienda Taboga, 7 mi. S.W. of Cañas, Guanacaste Prov., Costa Rica and a wooded pond near Rincon, Puntarenas Prov., C.R. Both Costa Rican areas were studied during the wet season, July and August, 1970, respectively.

CENSUS AND MARKING

Adult *Micrathyria* were counted at each of the three principal sites, as described in a previous paper (MAY, 1977). During each census, air temperature and other weather conditions were recorded when appropriate. At Pedro Miguel it was impossible to census the entire perimeter of the pond, so two separate sections, one at the west end (~25 m) and one at the east (~50 m), were studied.

In January 1977, specimens of *atra* at Ocelot Pond, *aequalis* at Summit Gardens, and *ocellata* at Summit Gardens and Pedro Miguel were marked with enamel paint for individual recognization (CAMPANELLA & WOLF, 1974). After release, free-ranging, marked individuals could be recognized with binoculars. The presence of marked specimens was noted during each census circuit. At Summit Gardens only, the position of each dragonfly was recorded on a map of the pond being censused (MAY, 1977).

OBSERVATION OF AGGRESSIVE BEHAVIOR AND PERCH OVERLAP

I watched individual *M. ocellata* continuously for fifteen minute intervals, on several days at Summit Gardens Pond 3 in January 1977, from 08:20 - 17:30, and recorded the number of aggressive interactions with other dragonflies. Total observation time was six hours. Individuals were occasionally out of sight briefly, and if interaction occurred during these intervals they were, of course, not recorded. Whenever possible, marked individuals were observed. Otherwise, I assumed that any *ocellata* returning to the immediate vicinity of the initial perch was the original individual being watched.

On two days, the nature and height above the water of each perch occupied by *aequalis* and *ocellata* at the pond was recorded at intervals. Perch height was estimated visually to the nearest 2.5 cm below and 7.5 cm and to the nearest 7.5 cm at greater heights.

GUT CONTENTS

Specimens of *M. atra* were collected at Ocelot Pond at various times on three different days in January 1977, and immediately preserved in 85% ethanol. Groups of *ocellata* were collected at Pedro Miguel at two hour intervals from 07:30 - 15:30 on 26 January 1977 and at 17:30 on 23 January, and likewise preserved in alcohol. The gut contents were later examined by sectioning each specimen mid-sagitally, noting the position of the food, removing the contents as thoroughly as possible with fine forceps, drying at 90°C overnight, and weighing to 0.1 mg.

RESULTS

OCCURRENCE AND ACTIVITY OF SPECIES

Species of *Micrathyria* recorded at the Panamanian sites were: Summit Gardens - *M. aequalis* (mean length of hind wing = 23.5 mm), *M. atra* (rare; h.w. = 32.0 mm), *M. laevigata* (rare; h.w. = 27.5 mm), *M. ocellata* (h.w. = 25.5 mm), *Micrathyria* sp. A (near *eximia*[1]; h.w. = 19.5 mm), and *Micrathyria* sp. (unidentified, rare; h.w. = 22.0 mm); Ocelot Pond - *M. aequalis*, *M. atra*, *M. didyma* (rare; h.w. = 30.5 mm), *M. laevigata*, *M. ocellata*, *M. tibialis* (rare; h.w. = 20.0 mm), *Micrathyria* sp. B (near *mengeri*[1]; h.w. = 24.5 mm); Pedro Miguel - *M. aequalis*, *M. ocellata*, *Micrathyria* sp. B (rare). Species recorded in Costa Rica were: Hacienda Taboga - *M. hageni* (h.w. = 28.0 mm), *M. schumanni* (h.w. = 26.5 mm); Rincon - *M. atra*, *M. dictynna* (h.w. = 26.0 mm), *Micrathyria* sp. A. In the lists above, mean hind wing length, from museum specimens, is used as a convenient index of relative size.

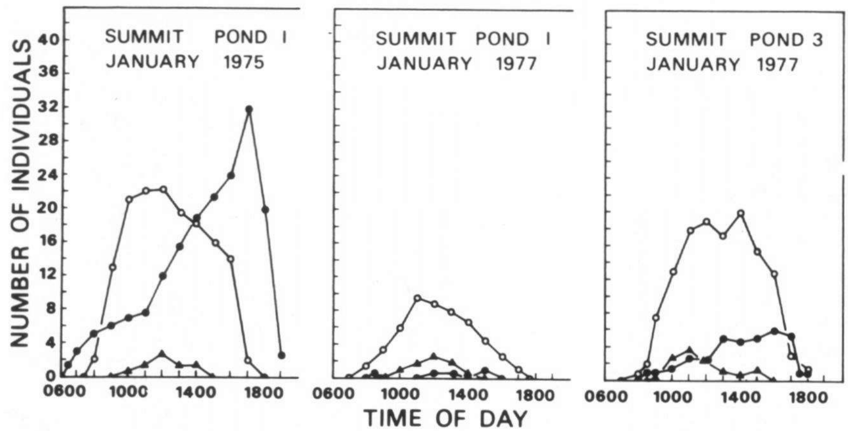

Fig. 1. Numbers of individuals of three *Micrathyria* species present at Summit Gardens in January 1975 and January 1977. Symbols are: *M. aequalis* - open circles, *M. ocellata* - filled circles, *Micrathyria* sp. A - filled triangles. Data for Pond 1, 1975, were presented previously (MAY, 1977).

Figures 1-4 summarize data on activity patterns in adults of *aequalis*, *atra*, *ocellata* and *Micrathyria* sp. A. Considerable variation is apparent between sites and from year to year at a given site. Previous work showed large

[1] Dr. M.J. Westfall has compared specimens of these species with the types of *eximia* and *mengeri* and concluded that they represent undescribed species.

seasonal fluctuations (MAY, 1977). For example, in January 1977, *ocellata* males at Summit Pond 3 (Fig. 1) exhibited a distinct late afternoon peak of activity, whereas at Pedro Miguel (Fig. 3) activity was more or less bimodal. *M. aequalis*, on the other hand, consistently was present in greatest numbers at about midday.

Summit Ponds 1 and 3 are very similar and located less than 100 m apart; nevertheless, in 1977, considerably more *aequalis* and *ocellata* were present on Pond 3. The difference in density of the populations on the water was even greater, as Pond 3 is smaller. On the other hand, Figure 2 shows that in May, 1974 maximum numbers and timing of activity were quite similar for all three species (although density was still highest on Pond 3). Such similarity was probably the rule (personal observations, 1972-1975).

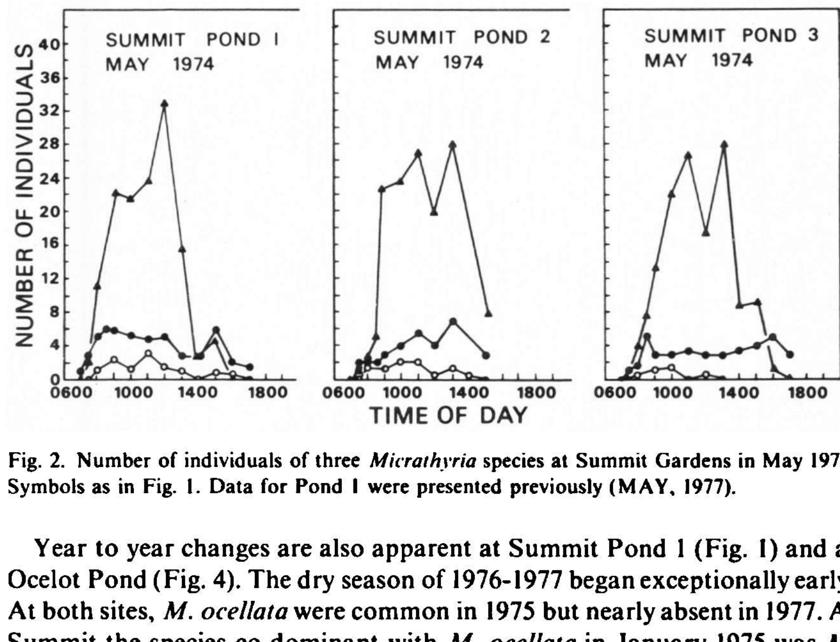

Fig. 2. Number of individuals of three *Micrathyria* species at Summit Gardens in May 1974 Symbols as in Fig. 1. Data for Pond 1 were presented previously (MAY, 1977).

Year to year changes are also apparent at Summit Pond 1 (Fig. 1) and at Ocelot Pond (Fig. 4). The dry season of 1976-1977 began exceptionally early. At both sites, *M. ocellata* were common in 1975 but nearly absent in 1977. At Summit the species co-dominant with *M. ocellata* in January 1975 was *M. aequalis*. In 1977 *aequalis* showed a nearly identical temporal pattern of activity and somewhat reduced density. Numbers and activity patterns at Summit Pond 1 in January 1972-1974 appeared similar to those observed in 1975, although I made no censuses. At Ocelot Pond the co-dominant was *M. atra* in 1975. This species was equally abundant in 1977 but shifted from an early morning to an early afternoon peak of activity, about 5 hours later than in 1975. Some individuals nevertheless appeared before 06:30. As previously reported (MAY, 1977), the latter flew continuously until ambient

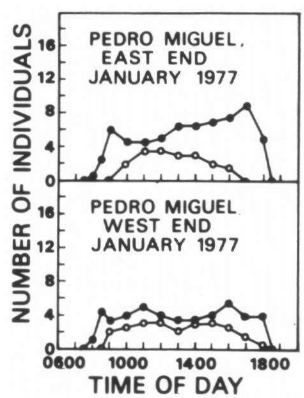

Fig. 3. Number of individuals of two *Micrathyria* species at two areas on an artificial pond near Pedro Miguel in January 1977. Symbols as in Fig. 1.

temperatures exceeded 23°C. The early appearance of *atra* seems independent of temperature, but *ocellata* is probably affected somewhat by temperature; e.g. the first peak of activity at Pedro Miguel occurred about one-half hour earlier at the west end, which received the earliest morning sun, than at the east end. Some additional observations at this site suggest that arrival may be later on cooler mornings.

Observations were sufficient for a qualitative description of activity pattern of several other species. At Rincon, C.R., *atra* individuals first appeared between 06:00 and 06:30 and activity reached a maximum at about 10:00. Thereafter cloudy conditions and intermittent rain prevailed on most days, and few individuals were present. On one day without rain, numbers remained high until the last census, at 13:00.

At Hacienda Toboga, C.R., both *M. schumanni* and *M. hageni* were present by 06:30 and most individuals were in continuous flight at that time, although a few perched. Ambient temperature was 23-24°C. By 07:30 these species were perching freely. The early arrival and initial period of flight resembled the behavior of *atra* and *ocellata* in Panama. *M. hageni* and *M. schumanni* both were active until 16:30 when observations terminated.

Micrathyria sp. B, a species sharing the wooded habitat of *atra*, but similar in size to *ocellata* (MAY, 1977) was observed primarily at Ocelot Pond. It did not appear at the pond until after about 08:30 and never flew continuously for long periods. I recorded it only as late as 12:30, but it probably was present later. The species was at Ocelot Pond from May - September 1974 and in January 1977 (but not Jan. 1975) and at Pedro Miguel in January 1977.

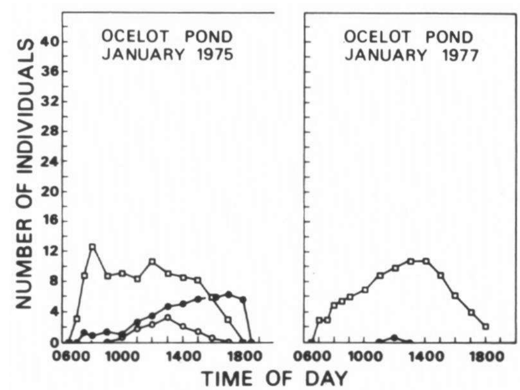

Fig. 4. Numbers of individuals of three *Micrathyria* species at Ocelot Pond in January 1975 and January 1977. Symbols as in Fig. 1; open squares designate *M. atra*. Data for 1975 were presented previously (MAY, 1977).

Finally, *M. laevigata* was

unusual in that most individuals observed, although apparently mature, were not reproductively active. Occasionally males holding territories were noted, but must seen, females (primarily) and males perched on plant stems 10-20 m from one end of Ocelot Pond in January 1975 and January 1977. First appearance was usually about 07:00 but as late as 12:00 on one occasion. Numbers ranged from 1-4, and all disappeared by 17:00 - 18:00. Similarly, on Barro Colorado Island, on several occasions in February 1974 seemingly mature males and female specimens of *M. didyma* were seen perching far from any water during the middle of the day.

OCCURRENCE OF FEMALES

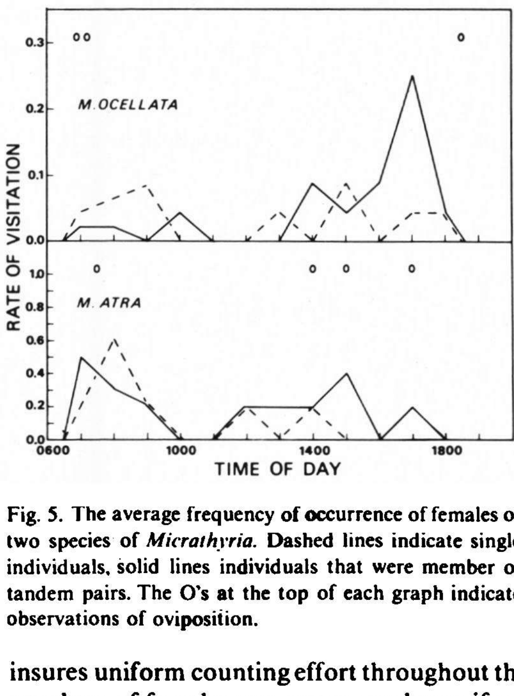

Fig. 5. The average frequency of occurrence of females of two species of *Micrathyria*. Dashed lines indicate single individuals, solid lines individuals that were member of tandem pairs. The O's at the top of each graph indicate observations of oviposition.

At almost any given time the great majority of individuals at all breeding sites were males, except in *laevigata*. Females appeared only briefly to mate or oviposit, most often during times of greatest male activity. Date on female occurrence, in *aequalis* and *Micrathyria* sp. A were presented earlier (May, 1977). Some additional and some reanalyzed data are presented here for *M. atra* and *M. ocellata* (Fig. 5).

These data are from all day censuses (except some records of *ocellata* females from partial censuses in March and May 1974). This insures uniform counting effort throughout the day. Data are plotted as mean numbers of females per census per hour; if more than one census was taken within an hour on a given day results were averaged and the average treated as a single value in arriving at the mean for the time period.

Frequency of *ocellata* females was distinctly bimodal, with a minor peak at 08:00 - 09:00 and a major peak at 17:00. This follows the overall pattern of male activity. The proportion of females that were not members of tandem pairs when observed was distinctly higher in the morning. Although data are too scanty to permit extensive comparisons the early peak of female activity was just as pronounced during the dry season, when early morning temperatures were comparatively low, as during the wet season, when temperatures were several degrees warmer.

M. atra females visited more frequently than did *M. ocellata* females, partly because censuses of *ocellata* included periods of low overall abundance for the species (MAY, 1977) while all *atra* data were from periods of fairly high numbers. Nevertheless, substantially fewer females were available per male *ocellata* at almost any time. In *atra* females, as in *ocellata*, activity was bimodal, with peaks at 07:00 - 08:00 and at 14:00 - 15:00. The proportion of females not in tandem was highest in the early morning. The pattern of occurrence was similar in both January 1975 and January 1977 and was similar to male activity patterns in 1975 but not in 1977. In both species oviposition tended to occur before 08:00 or after 14:00. At Rincon, C. R., mated females of *M. atra* were observed during nearly half the censuses between 08:30 and 10:30, not at all from 11:00 - 12:30, and again at 13:00. Oviposition occurred from 08:30 - 11:00.

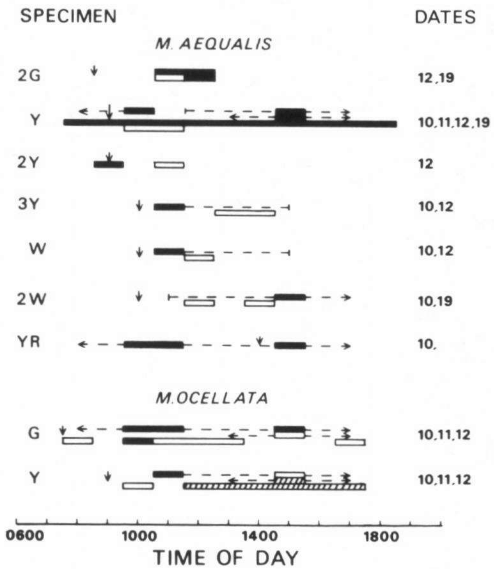

Fig. 6. Activity periods of individuals of *Micrathyria aequalis* and *M. ocellata* marked on 6 January and resighted on later dates in January 1977 at Summit Pond 3. The horizontal bars indicate times (± 0.5 hrs) that individuals were actually observed. Different patterns on these bars show time spent on different perches more than 3 m apart. Dashed horizontal lines span times when individuals were not seen due to intermittent observations, but may have been present; if these end in vertical lines, observations were made beyond that point and the individual was not present; if they end in an arrow, observations were not made and the maximum limits of the activity period are not known. Short vertical arrows indicate the time of day the specimen was marked. The letters to the left of the bar designate the individual to which the data pertain. The numerals to the right are the dates of resighting.

At Hacienda Taboga, C.R., mating occurred from 06:30 - 10:00 for *M. hageni*, and 07:00 - 12:00 for *M. schumanni*. In both species oviposition was observed only before 08:00. Since observations extended only until 16:30 late afternoon activity is not precluded.

ACTIVITY PATTERNS OF MARKED INDIVIDUALS

Figures 6-8 show times of breeding activity of individually marked male *Micrathyria*. Some individuals of *aequalis* and *ocellata* remained continuously at breeding sites for almost the whole day (up to 11 hours in *aequalis* Y, Fig. 6, and *ocellata* 2R, Fig. 7). Others remained more briefly, including some for only one to two hours, as must occur in any species with a sharp peak of activity. By contrast, *M. atra* individuals were present for only a few hours at a time (maximum of 5 hours, G in Fig. 8), and the composition of the population at Ocelot Pond probably changed completely two or three times on any given day. In both *atra* and *ocellata*, individuals occasionally left the ponds and returned later in the day (e.g. *ocellata* G, Fig. 6, and 2G, Fig. 7; *atra* RG, Fig. 8). The timing and duration of activity might change during the lifetime of an individual. For instance, *M. aequalis* Y (Fig. 6) was present for 11 hours on 12 January but for 2 hours on 19 January. *M. atra* Y visited Ocelot Pond from about 08:30 - 10.00 on 13 January and from 14:00 - 15:00 on 17 January.

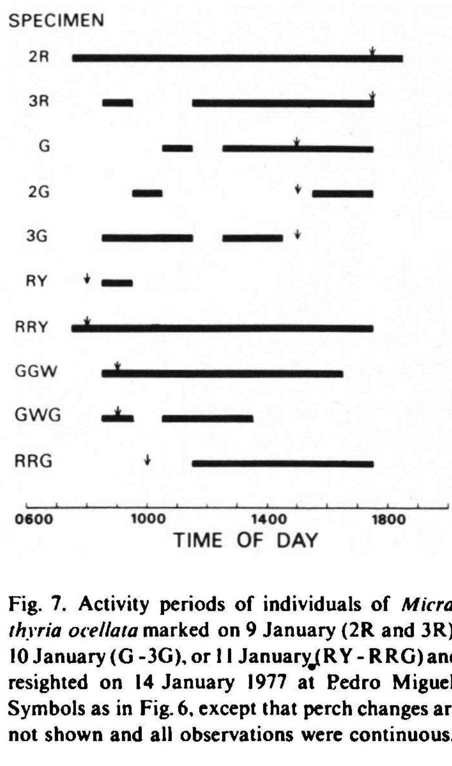

Fig. 7. Activity periods of individuals of *Micrathyria ocellata* marked on 9 January (2R and 3R), 10 January (G -3G), or 11 January (RY - RRG) and resighted on 14 January 1977 at Pedro Miguel. Symbols as in Fig. 6, except that perch changes are not shown and all observations were continuous.

At least in *M. aequalis* and *M. ocellata* individuals might be present for several consecutive days, but not necessarily on the same territory (e.g. *ocellata* Y, Fig. 6). On the other hand, individuals of *aequalis* and *atra* (and probably also *ocellata*; P. Campanella, personal communication) might be absent one or more days, then present on a later date (e.g. W, Fig. 8).

Both *M. aequalis* and *M. ocellata* changed the location of their territory within a pond, either in a single day or from day to day (Fig. 6). Sometimes, a brief absence from the pond preceded the switch (e.g. *ocellata* Y). *M. atra* individuals also changed territories; although not indicated in Figure 8 individuals RG returned to a completely different spot on the pond perimeter after its long absence on 13 January.

The species also differed in frequency of resighting and maximum elapsed time from marking to resighting. Of 16 *aequalis* marked on 5 or 6 January 1977, 7 were resighted at least once (44% resighting), 3 during the last census at Summit Gardens on 19 January. Of 8 *ocellata* marked at Summit on 5-6 January only 2 (25%) were resighted, none later than 12 January. None of the 6 *Micrathyria* sp. A marked were seen again. At Pedro Miguel, 10 of 31 marked *ocellata* (32%) were resighted on 14 January 1977, including two marked as early as 8 January. None were seen during the final census on 25 January. Resighting frequency was greatest for *atra*; 17 of 24 marked (71%) were resighted including one marked on 8 January and seen again twenty days later (W, fig. 8).

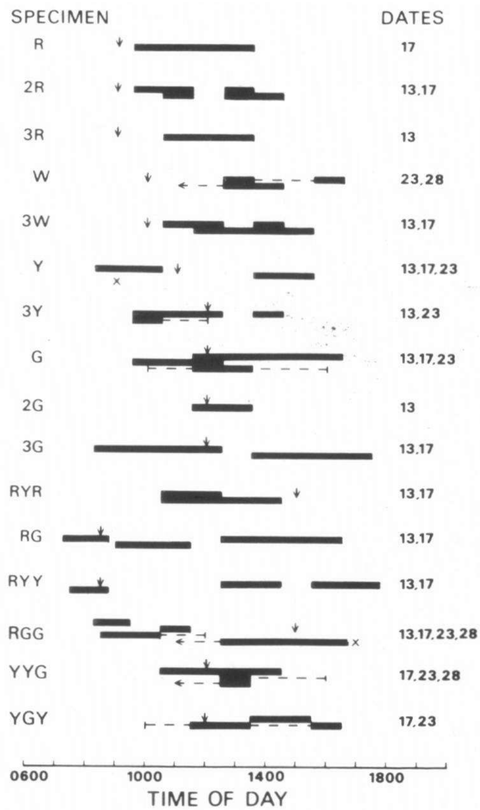

Fig. 8. Activity periods of individuals of *Micrathyria atra* marked on 8 Jan. (R - RYR), 9 January (RG - RGG), or 10 January (YYG and YGY) and resighted on later dates on January 1977 at Ocelot Pond. Symbols as in Fig. 6 except that perch changes are not shown.

PERCH CHOICE

Figures 9-10 indicate the *M. aequalis* and *M. ocellata* have distinctive preferences in both the height and nature of their perches. These figures do not give an exhaustive picture of perch selection, but, the data are fairly representative. *Micrathyria* sp. A at Summit used perches similar to *M. aequalis* and perched as low as or lower than the latter species, in general. At Ocelot Pond *M. atra* favored emergent sticks around the perimeter of the pond, usually higher than 30 cm. Thus members of this genus roughly follow the rule that perch height is proportional to body size (CORBET, 1963). A great deal of overlap exists in perch choice, however (Fig. 9-10). On several

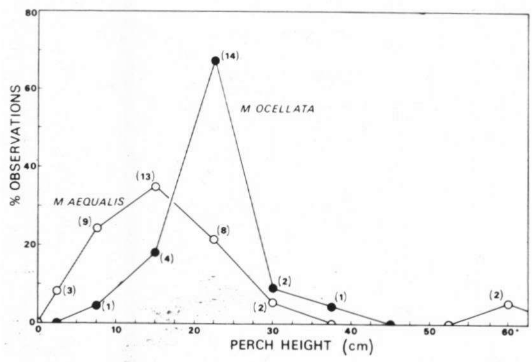

Fig. 9. Distribution of estimated heights of perches occupied by *Micrathyria aequalis* (open circles) and *M. ocellata* (filled circles) at Summit Pond 3 in January 1977. Numbers in parentheses indicate number of observations for each point.

occasions I saw individuals of different species succeed each other on the same perch within a short period of time.

At Summit, where perches were scattered generally over the pond surfaces, most of them more or less surrounded by water, dragonflies likewise were distributed over the entire pond. At Pedro Miguel, both *aequalis* and *ocellata* were practically restricted to the narrow region where emergent grasses met the open water of the pond center. Evidently only perches immediately overlooking open water were acceptable. This resulted in very different distributions of individuals at the two sites.

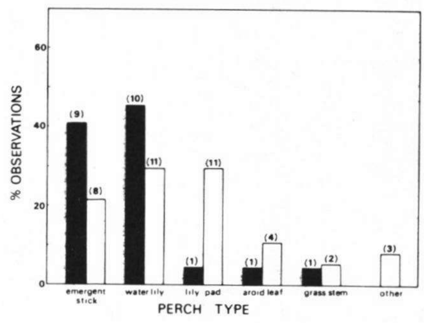

Fig. 10. Distribution of perch types occupied by *Micrathyria aequalis* (open bars) and *M. ocellata* (filled bars) at Summit Pond 3 in January 1977. Numbers in parentheses indicate number in each sample.

AGGRESSIVE INTERACTION

Interaction involving chasing and/ or fighting among male dragonflies were frequent in all *Micrathyria*, as shown in Table I for *ocellata*. *M. ocellata* males also made approximately 19.5 flights per hour that did not result in an obvious chase but that may have been elicited by the presence of other odonates.

The number of interactions of *ocellata* with *aequalis* was approximately proportional to the number of individuals of the latter species present (Fig. 11). More interactions with *aequalis* occurred than with any other species, including other *ocellata*. The rarity of *ocellata* - *ocellata* chases was undoubtedly due to the low density of the species at this site. *M. aequalis*

Table I
Aggressive interactions by *Micrathyria ocellata* at Summit Gardens Pond 3
(Total observation time = 6 hr)

Interacting species	No. of interactions
Coryphaeschna adnexa	4
Erythemis plebeja	12
Erythrodiplax connata	18
Micrathyria aequalis	33
M. ocellata	1
Perithemis mooma	4
unidentified Anisoptera	9
Zygoptera	1
Total	82 or 13.7 per hour

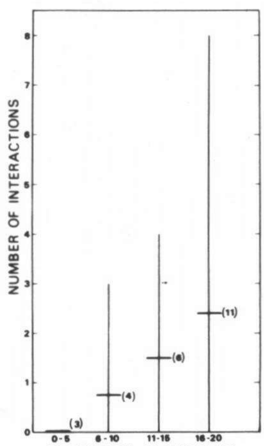

Fig. 11. Numbers of aggressive interactions of *Micrathyria ocellata* individuals with *M. aequalis*, as a function of the number of *M. aequalis* present. Horizontal bars indicate the mean, vertical lines the range of interactions for a given range of *M. aequalis* numbers. Data are from Summit Pond 3, January 1977.

elicited more responses from *M. ocellata* than did species of other genera, although without data on numbers of individuals of the other species it is impossible to determine whether this was only because of the higher density of *M. aequalis*. *Erythrodiplax connata fusca* appeared to be about as common as *M. aequalis*, however, yet was involved in only about half as many interactions with *M. ocellata*.

Both intra- and interspecific interactions were frequent among other species. *M. atra* and *M. ocellata* often chased one another at Ocelot Pond when the latter species was common. Even in January 1977, when *ocellata* was seen only twice, chases with *atra* ensued both times. In addition, *Orthemis ferruginea* often chased *M. atra*. At Hacienda Taboga, aggression appeared to be more frequent between *M. hageni* and *M. schumanni* than between either and other genera.

GUT CONTENTS

The position and approximate dry mass of gut contents of *M. atra* and *M. ocellata* at various times of day are shown in Figure 12. Determination of mass suffers from two types of inaccuracy. First, most specimens remained preserved in alcohol for almost two years before analysis, and some material may have been lost into solution. Second, removal of the contents with forceps was indoubtedly incomplete, and parts of the gut epithelium may have been included in the samples. Neither of these errors, however, was judged to be sufficient to obscure the overall trends or invalidate comparisons to be made.

Position of contents is indicated by tagma and segment number. Roughly speaking the esophagus extends through the thorax, the crop occupies abdominal segments 1-3, the midgut 3 or 4 to 7 or 8, and the hindgut the remaining segments (TILLYARD, 1917; and personal observations). Specimens containing large masses of food usually had full crops, as this was by far the organ with the largest lumen volume. In most individuals segment 9 contained no food material; the hindgut is greatly narrowed in this segment.

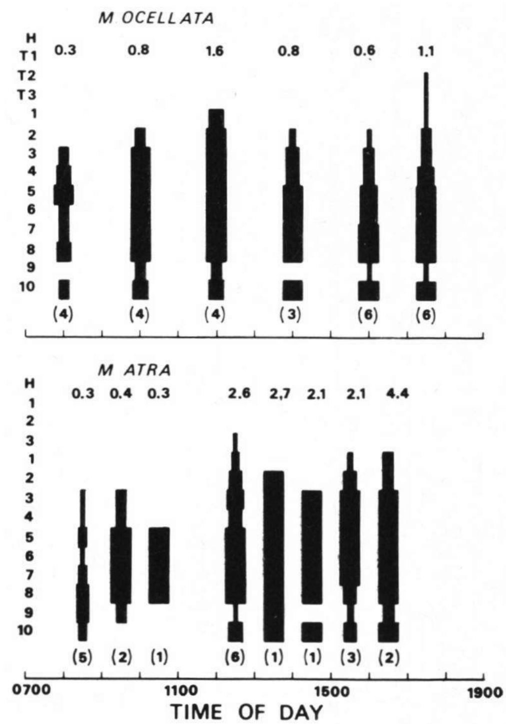

Fig. 12. Distribution of food within the alimentary tract of *Micrathyria ocellata* at Pedro Miguel and *M. atra* at Ocelot Pond as a function of the time of day the specimen was collected. The presence of food in the mouth or head (H), the thoracic segments (T1 - T3), and the abdominal segments (1-10) is indicated by a vertical bar. The width of the bar is proportional to the fraction of the total sample (size shown in parentheses below) that had food in that segment. The average dry mass (mg) of food in the entire gut is shown in figures above the corresponding bar.

In both species, diurnal variations in mass and position of contents were consistent. In *atra* specimens collected before 11:00 had less than 0.5 mg contents and empty crops. After 12:00 specimens generally contained more than 2 mg and had food in the crop, or, in one case, the esophagus. In *ocellata* from Pedro Miguel, the quantity of food and proportion of individuals with full crops increased throughout the morning until 12:00, thereafter declined until 16:00, but increased again at 17:30. One individual taken at the latter time had food throughout the posterior esophagus, probably indicating that it had fed quite recently.

DISCUSSION

What factors dictate the timing of activity in *Micrathyria*? I assume that the daily activity patterns of a species at a given time and place reflect the average relative costs and benefits of activity at a particular time of day; i.e. most individuals will be present at a time when benefits (primarily the opportunity to mate, or, for females, to oviposit) maximally exceed costs. The activity patterns of a specific individual may also reflect constraints peculiar to that individual, e.g. its ability to hold a territory under competitive conditions, its energy resources, etc. (CAMPANELLA & WOLF, 1974). It is within this frame of reference that answer will be sought.

SPECIES ACTIVITY PATTERNS

One factor that may greatly influence the cost of breeding activity is the physical environment, especially temperature. The response to temperature of several of the species considered here were discussed in an earlier paper (MAY, 1977). I found that *M. atra* and, to a lesser extent, *M. ocellata*, thermoregulate at low ambient temperatures by remaining continuously in flight, while *M. aequalis* and *Micrathyria* sp. A do not. Thus it appeared that the latter two species were restricted primarily to the period from mid-morning to mid-afternoon while the former attained a degree of independence from temperature constraints and were potentially more flexible in activity periods. None of these species seemed limited by high temperatures. The present data are consistent with this analysis. *M. aequalis* and *Micrathyria* sp. A, in particular, are rather constant in activity patterns in a variety of circumstances, although individuals of *aequalis* were more evenly distributed throughout the day at Pedro Miguel than at Summit. The failure of a sharp peak of activity to develop at this site may have been influenced by wind, which rose to velocities of 10 m/sec during the middle of the day and sometimes visibly interfered with normal behavior. *M. ocellata*, by contrast, had an early peak of activity at Pedro Miguel but not at Summit, although temperatures at the two sites did not differ appreciably. *M. atra* markedly altered its activity patterns at Ocelot Pond from January 1975 to January

1977, although the temperature regime was no different, and a few *atra* were active very early in 1977. Thus it appears that temperature and other physical factors may largely determine the activity periods of small species like *aequalis*, have a considerable but not overwhelming effect on *ocellata*, and be of secondary importance in larger species like *atra*. *M. hageni* and *M. schumanni*, species intermediate in size between *ocellata* and *atra*, both commenced activity very early and flew a disproportionate amount of time at low temperatures. These observations reinforce the suggestion that larger species of *Micrathyria* are endothermic and thus escape temperature restrictions to some extent. Such temperature independence may be attainable at less energetic and evolutionary cost in the thermally equable tropics than in the temperate zone.

Another major cost of breeding activity may be the expenditure of time and energy and the risk of injury consequent to conflicts with other individuals. Interspecific clashes may favor shifting of peak activity to reduce overlap, if physical conditions permit. I suggested earlier (MAY, 1977) that *M. atra* and *M. ocellata* may shift their activity maxima to times when their relative competitive advantage over congeneric species is greatest, and that this response should be influenced by the population density of the other species. The present data tend to bear this out, although additional confirmation is needed.

First, different species overlap considerably in perch choice (Figs. 9-10). This does not mean that the number of perches is actually limiting — there is always a considerable excess of perches — but it does mean that congeneric individuals may often tresspass on the defended area of one another. Aggressive encounters, and thus the cost of coexistence, increased markedly with density (Fig. 11).

The variations in patterns of activity in *M. atra* and *M. ocellata* may also be more understandable when the density of potentially competing species is examined. Especially striking is the change in time of maximum activity of *atra* from January 1975 to January 1977. This could be explained if *M. atra* and *M. ocellata* shifted away from each other to avoid excessive conflict in 1975, then *atra* moved into the period that was most attractive from the standpoint of physical conditions when *ocellata* was absent.

The contrast between the temporal distribution of *M. ocellata* at Summit Pond 3 and at Pedro Miguel in 1977 possibly exemplifies a similar adaptive shift in maximum activity. At Summit, when *aequalis* outnumbered *ocellata*, peak numbers of the latter were present well after the peak of *aequalis* activity. At Pedro Miguel, however, *ocellata* always exceeded *aequalis* in numbers and at maximum were about twice as abundant. Thus at Summit interspecific conflicts may have been relatively more important than at Pedro Miguel, where intraspecific competition must have been greatest. It seems possible, therefore, that the early peak of activity and relatively high plateau during the middle of the day was possible because of the reduction in competition with *M. aequalis* and was favored by intraspecific competition for space and for females.

The activity pattern of females may be an important selective force on the timing of activity in males (MAY, 1977), since mating is the raison d'être of the males' presence at the pond; females must oviposit as well as mate and may be most successful at the former when few males are present (CORBET, 1963). I observed one female *M. atra* that visited Ocelot Pond at a time (14:30) of high male activity, flew low over the water as if to oviposit, but was chased from the pond after rejecting the copulatory attempt of a male. On the other hand, ovipositing *atra* females twice were successfully taken in tandem.

Females of *aequalis* and *Micrathyria* sp. A appeared only during the middle of the day, just as the males (MAY, 1977). This again is consistent with limitation of activity by physical conditions. In *ocellata* and *atra*, however, females seemed relatively more likely to be active early in the morning. The early activity persisted in both species even when male numbers were quite low at this time. Early activity was also characteristic of *hageni* and *schumanni* females. Oviposition, especially, was most frequent before or after peak male activity. The tendency toward very early onset and peak of ♀ visitation rate may explain why some males always appeared very early, even when peak male numbers were in the afternoon (MAY, 1977) and in part why *ocellata* males exhibited a bimodal acitivity at Pedro Miguel.

INDIVIDUAL ACTIVITY PATTERNS

The patterns of activity characteristic of species are, of course, simply the sums of a series of individual activity periods. These individual periods may be combined in various ways to produce a species pattern, so only by individual marking can individual activity be accurately inferred. The data on marked individuals are preliminary, but some tentative conclusions may be drawn.

The elapsed time from marking to last sighting was markedly lower in *M. ocellata* than in the other two species. Numbers of *ocellata* at Summit were much lower than in previous years, so the population of this species may have been declining at the time of these observations. In that case, the comparatively rapid disappearance of marked individuals might not be characteristic of the species at other times. P. Campanella (personal communication) has observed individuals of *ocellata* several weeks after marking.

It is of particular interest that in *M. atra* all individuals stayed for comparatively short periods while in *M. aequalis* and *M. ocellata* some individuals were present all day. The average energetic cost of activity is considerably higher in *atra* than in the other species (MAY, 1977), partly because of the greater expenditure devoted to endothermy and partly because even under warm conditions they tend to spend more time in flight than either *ocellata* or *aequalis*. Perhaps this greater energy expenditure necessitates shorter daily periods devoted to breeding than in other species. Note that both individuals (RG and RYY, Fig. 8) first appearing before 08:00 were present initially for not more than 1½ hrs (RG returned in the afternoon). These were specimens most likely to have been expending energy at a very rapid rate while thermoregulating.

HIGASHI (1978) estimated that in *Sympetrum frequens* the half time for food passage through the gut was between one and two hours. If *Micrathyria* are at all similar to *Sympetrum*, then the following interpretation is consistent with the observations of gut contents. *M. atra* present before 11:00 had fed little, if any on the day of capture, while those captured later had fed the same day. No decline in contents occurred during the afternoon because of the steady turnover of individuals. In *M. ocellata* specimens caught very early had not fed, but the chance of an individual having fed increased through the morning. Thereafter, the decline in contents perhaps reflected depletion of gut contents in individuals continuously present at the pond. The late peak in gut contents may have resulted from the late influx of new individuals (Fig. 3); presumably these had been feeding away from the pond. In both species the results support the casual observation that individuals do not feed at breeding sites and therefore must be depleting energy reserves. This is not to say that dragonflies depend directly on gut contents for energy, as they almost surely store lipids (KALLAPUR & GEORGE, 1973), but it does emphasize the fact that long periods of high energy expenditure at breeding areas may make it difficult to maintain a positive energy balance. The presence of considerable food in the alimentary tract of most *M. atra* in the afternoon suggests that the fairly rapid turnover of individuals allowed them to replenish their energy supply.

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REFERENCES

CAMPANELLA, P.J., 1975. The evolution of mating systems in temperate zone dragonflies (Odonata: Anisoptera). II: Libellula luctuosa (Burmeister). *Behaviour* 54: 278-310.

CAMPANELLA, P.J. & L.L. WOLF, 1974. Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera). I. Plathemis lydia (Drury). *Behaviour* 51: 49-87.

CORBET, P.S., 1963. *A biology of dragonflies.* Quadrangle Books, Chicago.

HIGASHI, K., 1973. Estimation of the food consumption for some species of dragonflies. I. Estimation by observation for the frequency of feeding flights of dragonflies. *Rep. Ebino Biol. Lab.* 1: 119-129.

HIGASHI, K., 1978. Daily food consumption of Sympetrum frequens Selys (Odonata: Libellulidae). *JIBP Synthesis* 21.

KALLAPUR, V.L. & C.J. GEORGE, 1973. Fatty acid oxidation by the flight muscles of the dragonfly, Pantala flavescens. *J. Ins. Physiol.* 19: 1935-1940.

LUTZ, P.E. & A.R. PITTMAN, 1970. Some ecological factors influencing a community of adult Odonata. *Ecology* 51: 279-284.

MAY, M.L., 1977. Thermoregulation and reproductive activity in tropical dragonflies of the genus Micrathyria. *Ecology* 58: 787-798.

MAY, M.L., 1978. Thermal adaptations of dragonflies. *Odonatologica* 7: 27-47.

NELEMANS, M., 1976. Aktiviteitsritmiek bij libellen in Noord-Zweden (64°N). [Abstract]. *Odonatologica* 6: 134.

PEZALLA, V.A.M., 1977. *The behavioral ecology of a dragonfly, Libellula pulchella.* Ph.D. Thesis, Univ. Minnesota.

TILLYARD, R.J., 1917. *The biology of dragonflies.* Cambridge Univ. Press, Cambridge.