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ORIENTATION AND REPRODUCTIVE CONDITION OF MIGRATING DRAGONFLIES (ANISOPTERA)

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From equatorial Uganda and southern Canada the behaviour and reproductive condition of migrating Anisoptera are described. In neither situation was sexual activity seen among migrating adults. In Uganda, a very large flight of Anisoptera, predominantly *Hemianax ephippiger*, descended at sunset from a great height, roosted overnight and then left at sunrise. Females among these *H. ephippiger* were unmated, very immature reproductively, and richly endowed with abdominal fat. They, and 2 other spp. accompanying them, probably began migrating in the early post-teneral stage. In Canada, aggregations of Anisoptera, mainly *Anax junius*, were observed as they roosted in Aug. and Sept. on their way south. Adult *A. junius* roost on west-facing vegetation but exhibit a brief, pre-sunrise adjustment flight by which they move to east-facing perches that relatively quickly become warm. It is suggested that not only migrants may benefit from such a translocation early in the morning; moreover it may be useful for orientation during migration, whether or not it is necessitated by low ambient temperature. All (female) *Tramea lacerata*, almost all *A. junius* and most *Pantala flavescens* examined from these aggregations were immature reproductively and almost all *Sympetrum vicinum* were mature. Abdominal fat correlates moderately well with ovarian immaturity in *A. junius* but not in the 3 other spp. examined.

INTRODUCTION

Occasionally, while in Uganda and Canada, I observed dragonflies stopping overnight during migration. In this account I focus on their behaviour during arrival, roosting and departure, and on their reproductive condition. In doing so, I document fully aspects that have been noticed briefly elsewhere (CORBET, 1974; CORBET & EDA, 1969).

The terms "sunrise" and "sunset" are used in the precise sense and denote a time when under a clear sky the incident light intensity is about 2.80 log lux; at civil twilight, when the sun is about 6° below the horizon, the corresponding value is about 0.55 log lux (NIELSEN, 1963).

THE UGANDA SIGHTING

At Entebbe, Uganda (0°3'N, 32°59'E) many species of inter-tropical migrants appear and disappear with the seasonal rains. These migrants include most of the East African dragonflies that are assumed to travel with the Inter-Tropical Convergence Zone (ITCZ) (CORBET, 1962). During October (especially), November and December 1961 large numbers of such dragonflies (predominantly *Pantala flavescens* (F.)) arrived intermittently in Entebbe, which in October had experienced the heaviest and most prolonged "short" rains since records began 60 years before. On January 29 and 30, 1962 I witnessed the arrival and departure of a large migration in the compound of the East African Virus Research Institute, Entebbe.

ARRIVAL AND DEPARTURE

While straining to keep a soaring hawk in sight, I first noticed high flying dragonflies, from 50 to several hundred feet above the ground, at 1820 hr East African Standard Time (sunset fell at 1905 hr and civil twilight at 1926 hr E.A.S.T.). I had not seen any at such a height at 1805 hr; but many thousands of Anisoptera had been passing through the compound near the ground from about 1500 hr (E.A.S.T.) that day. As the sun set, the high-flying dragonflies descended steadily, appearing to darken the sky as they did so. They levelled out at 5-20 feet above the ground when I could see that the flight consisted predominantly of *Hemianax ephippiger* (Burm.) and included a very few *Pantala flavescens* and *Tramea basilaris* (P. de Beauv.). Near the ground the dragonflies kept consistently to one direction, almost due east, rising to clear low hedges. They fed (in flight) only occasionally and briefly.

Between about 10 min before, and 10 min after, sunset the dragonflies settled on trees, including *Pseudocarpus*, not necessarily on the western side (as is normal for *P. flavescens*). They preferred branches about 20 feet high. Competition for branches was intense: there was many a noisy clash as a latecomer tried to settle on a resident's abdomen which would then be raised abruptly in the defence posture. Eventually roosting adults were closely packed, about 6-7 per foot on some branches, their outstretched wings being conspicuous against the sky. Considerable rustling and jostling continued until civil twilight.

The next morning, 15 min before sunrise (at no more than 1.36 log lux), these adults (predominantly and perhaps wholly *H. ephippiger*) briefly fluttered their wings and then began to fly from the roosting sites, there being a large, almost synchronous departure 5 min before sunrise (at no more than 2.28 log lux). After taking off, they flew steadily higher until lost to sight, keeping to a well defined direction which was indistinguishable from the one they had been following on arrival the previous evening.

REPRODUCTIVE CONDITION

Throughout the dragonflies' visit a mercury-vapour light-trap was operating in the Institute compound. Near this trap during the evening (and in the trap at known times — expressed as Solar Time, such that sunset and sunrise are at 1800 and 0600 hr respectively) the following species were caught: *H. ephippiger* — 20 ♂ 46 ♀ near the trap (1 ♂ in the trap: 00-01 hr); *Philonomon luminans* Karsch — 21 ♂ 27 ♀ (4 ♂ 3 ♀: 21-06 hr); *T. basilaris* 6 ♂ 9 ♀ (1 ♂ 1 ♀: 21-22 hr); in addition 2 ♂ and 5 ♀ *H. ephippiger* were collected from roosts about 50 yards from the trap and out of sight of it. This material provided information on reproductive condition.

Hemianax ephippiger. In both sexes: all adults appeared the same with respect to maturity; the wings were firm, unworn and non-glistening and there was a light fulvous tinting near the anal area of the hind wing; none bore copulation (or more correctely "tandem") marks (CORBET, 1962, p. 166); all dissected (2 ♂ 25 ♀) had extensive masses of yellowish-gold globular fat pervading the abdomen. In males: the dorsum of abdominal segment 2 was sky blue. In females: all dissected (25) had rudimentary, barely discernible ovaries thickly surrounded by fat; in one ovariole there were 18 follicles none of which contained yolk granules visible at X 40 magnification. Unfortunately gut contents were not recorded. However an observation made 9 days earlier at nearby Zika Forest (0° 7'N, 32° 30'E) suggests that this species feeds actively while migrating. Outside this forest many adults were hawking swiftly over the dew-laden grass 10 min after sunrise. The female that I caught was immature, though teneral, and lacked tandem marks; her ovaries were very small and her gut was full of food.

Philonomon luminans. In all females dissected (3) the ovaries were small (though follicles were clearly formed) and closely surrounded by fat; the gut contained food.

Tramea basilaris. In the female dissected the ovaries were small, though more developed than in *H. ephippiger,* and in some follicles a little yolk was visible; the ovaries were surrounded by fat, though not so thickly as in *H. ephippiger;* the gut contained much food.

No sexual behaviour was seen among the migrant dragonflies.

DISCUSSION

Had I not been looking up into the sky between 1800 and 1830 hr on January 29 I would not have noticed that the migrants were descending from a great height. Such an event, though perhaps not uncommon among ITCZ travellers (cf. RAINEY, 1976), must frequently escape notice.

The persistence and consistency with which the *H. ephippiger* adults maintained direction indicated that they were navigating by a sun-compass sense: skylight polarisation patterns during twilight can be used as a navigational aid by birds (ABLE, 1982); there were not any obvious guideways visible on the ground (cf. DUMONT, 1977).

The three species mainly represented at roosts are among those that arrive in large numbers in western Tanzania at about 8° S soon after the onset of the rains, presumably being carried there with the ITCZ (STORTENBEKER, 1967).

Adults of *H. ephippiger* superficially appeared young though not necessarily immature. Yet the females certainly, and the males probably, were very immature and it can be safely assumed that they began to migrate early in the post-teneral stage (cf. JOHNSON, 1969), richly endowed with fat which could provide a ready source of fuel and water during the journey (KALLAPUR, 1976). The *T. basilaris,* which had larger ovaries and less abdominal fat than *H. ephippiger,* had been feeding actively, almost certainly within the previous 12 hours (cf. HIGASHI et al., 1979). It would be instructive to examine the condition of all these species immediately after emergence. Dennis Paulson (1983, pers. comm.) has suggested to me that the migratory status of papered specimens in collections could be inferred by looking for grease stains on the envelops.

The significance of the skewed sex ratio of *H. ephippiger* caught near the trap is not evident. The times at which adults appeared in the trap may show their susceptibility to disturbance when illuminated at night.

THE CANADA SIGHTINGS

Point Pelee National Park, Ontario (41° 57'N, 82° 31'W) is a peninsula projecting south into Lake Erie. Each autumn large numbers of birds and insects congregate there briefly before flying south (ROOT, 1912). Conspicuous among the migrating insects are the butterfly, *Danaus plexippus* L., and several dragonflies, notably *Anax junius* Drury, *Pantala flavescens* and *Tramea lacerata* Hagen (CORBET & EDA, 1969). There is evidence that adults of these 3 species appearing each autumn at Point Pelee (and elsewhere along the northern shore of Lake Erie) are the product of eggs laid in spring by adults arriving in Canada from the United States (WALKER & CORBET, 1978): (1) adults of the summer (non-resident) population of *A. junius* in southern Ontario and Quebec do not return to the emergence site after emergence in August and September (TROTTIER, 1966, 1971); (2) adults of *A. junius* aggregate and fly in large numbers along the northern shore of Lake Erie in September and appear in Point Pelee at the same time (NISBET, 1960); (3) *P. flavescens* larvae cannot survive a winter in southern Quebec (TROTTIER, 1967); and (4) I have found fresh (final-stage) exuviae of *T. lacerata* at Point Pelee at the end of August.

Against this background I describe observations made by me at Point Pelee in 1964 and 1968.

To trace ovarian development in the adult I distinguished three stages: in stage 1 the follicles in each of the many ovarioles are almost uniform in size (the condition in newly emerged females); in stage 2 some basal follicles are larger than the rest; and in stage 3 many basal follicles have matured to their final shape, size and colour (the condition in females ready to lay eggs).

ROOSTING

On September 5, 1964, during the 3 hours before sunset (which was at 1840 hr Eastern Standard Time), many Anisoptera were hawking along the lee (east)

shore. *A. junius* (stage 1; 4 examined) predominated and remained spontaneously active until 100 min before sunset when many began to alight on west-facing trees (mainly cedar), shrubs and grasses. This continued increasingly until observations ceased 40 min before sunset. Also hawking there were *P. flavescens* and *T. lacerata* (stage 1; 1 of each). A female of *Sympetrum vicinum* (Hagen) was in stage 3.

On September 6, at least 30 min before sunrise (which was at 0601 hr E.S.T.), *A. junius* (resting on the west side of roosting sites) began spontaneously to vibrate their wings. At 24 min before sunrise (4 min after civil twilight) the first of them was seen to fly spontaneously. Their flight was rapid and darting; they soon settled low on grasses and herbs facing east, thus having moved from shaded to potentially insolated sides of vegetation. The first *T. lacerata* in flight was seen 25 min after sunrise. At about this time 6 *A. junius* (all facing east) were able to fly immediately (4) or after vibrating the wings for only 1-4½ min (2).

On August 28, 1969 I made similar, though more detailed, observations on the pre-sunrise movement of *A. junius* from the west to the east sides of roosts (cf. CORBET & EDA, 1969). On this occasion, at an air temperature (at 1 m) of about 13° C, adults were flying very rapidly 15 min before sunrise. From 11-47 min after sunrise hardly any were seen flying, and the west-to-east movement appeared to have been completed. Not until 65 min after sunrise (at about 17° C) did they again fly spontaneously; and then when they settled it was close to the now warming ground, with the dorsal surface of the abdomen facing the rising sun. Before sunset they had alighted on the west side of vegetation and those arriving later settled progressively higher as the sun set; at sunrise they had alighted on the east side and those arriving later settled progressively lower as the sun rose.

REPRODUCTIVE CONDITION

In September 1964 I examined females from beside a highway east of Toronto, and from Point Pelee; I also visited Pelee Island (the southernmost part of Canada) 16 miles south of Point Pelee in Lake Erie, where on September 11 in mid-afternoon in the lee of a copse I flushed many almost teneral *T. lacerata* and a few *A. junius*, all of which had ovaries in stage 1.

In August 1968 Anisoptera encountered by CORBET & EDA (1969) were noted as being "immature" or "mature". Here I report the results of dissections of females which amplify these designations. None of the *A. junius* in ovarian stages 1 or 2 possessed tandem marks but those in stage 3 did.

Material examined came from the places listed below (for locations of the Parks see CORBET & EDA (1969)).

H: Beside Hwy 401, 60 mi east of Toronto, Sept. 2, 1964; feeding actively.

PA: Point Pelee National Park, Sept. 5-10, 1964.

L: Long Point Provincial Park, Aug. 25, 1968.
R: Rondeau Provincial Park, Aug. 26, 1968.
PB: Point Pelee National Park, Aug. 27-28, 1968.

The number of females dissected from each site is given in brackets. The amount of abdominal fat (visible at about X 10 magnification) was recorded under three categories: much; some; and little.

Anax junius. H (2); PA (1); L (7); PB (16). Two, from PB, bore copulation marks, were in stage 3 and contained some and little fat. The rest were in stage 1 or 2 and the 21 scored for fat contained much (5), some (11) and little (5); in some specimens the small ovaries were thickly surrounded by fat.

These observations can be compared with the ovarian condition of 2 newly emerged adults obtained by me from the population studied in Quebec by TROTTIER (1966) and which consisted only of migrants. Both females were teneral and the abdomen was not yet fully expanded. The ovaries were small (about 5-10 mm long), very inconspicuous, and recognisable at low magnification by the ribbed texture of individual ovarioles lying parallel to the long axis of the ovary. The ovaries were pressed against the dorsum of abdominal segments 2 and 3 by muscle attached to the cuticle. Each ovariole was clearly delimited and individual follicles were distinct and in stage 1. Unfortunately these females were not scored for abdominal fat.

Pantala flavescens. PA (5); PB (4). Two, from PA, were in stage 3. The rest were in stage 1 or 2. Fat was not recorded but it was not conspicuous.

Sympetrum vicinum. PA (1); L (20); PB (4). One, from L, was in stages 1 and 2. The rest were in stage 3 and contained some (6) and little (18) fat; in some females eggs filled the abdomen (one contained 1074 eggs); others contained only a few eggs and so were clearly parous; in some specimens, eggs in the posterior part of the oviducts were dark brown with hard shells.

Tramea lacerata. L (1); R (11); PB (3). All were in stage 1 or 2 and contained little fat.

DISCUSSION

The ability of roosting *A. junius* to change from the west to the east side of vegetation just before sunrise is an elegant way of mitigating the effects of cool autumn nights when migrating. Were the roosting dragonflies not to change position at this time they would start the day in shade; by moving they perhaps achieve a gain in solar heating of the abdomen without great metabolic expenditure. The way in which the movement is accomplished shows the importance first, of wing-whirring as a means of endothermic warming, and second, of a behaviour pattern whereby warm-up and take-off are associated with, and perhaps induced by, very low (i.e. pre-sunrise) light intensities. The existence of such a response in an aeshnid has been noted elsewhere (CORBET, 1962, p. 134) in another context — that of a persistence in early adult life of the pre-sunrise activity that prefaces the maiden flight. Two possibilities to be

considered are first, that the pre-sunrise flight is triggered by an endogenous "clock", set the previous evening, and second, that, as some adults become active, they stimulate others nearby. It may be significant that several migratory species of tropical Anactini commonly exhibit crepuscular activity (cf. LIEFTINCK, 1954, pp. 109, 111; 1962, p. 45).

Perhaps pre-sunrise activity occurs widely in large Anisoptera that roost close to foliage. It is probably usual for such dragonflies to roost on west-facing surfaces in the evening. To start the day in shade, and sometimes also dew-laden (JURZITZA, 1964; JUDD, 1974), must impose a metabolic cost, especially in late summer or autumn, whether or not the insect is migrating. An additional possibility to consider is that orientation (to an east-facing position) may be readily accomplished at that time of day, either on account of patterns of sky polarisation (cf. departure behaviour of *H. ephippiger*), or simply because the first light clearly shows the direction toward which to orientate.

These considerations point to the value of noting the early-morning movements of dragonflies that roost on west-facing surfaces. Endothermic warming, followed by rapid relocation to an east face, may well constitute the behavioural counterpart of the specialised postural adjustments shown by species of *Austrolestes* that confer the ability to become active at low temperatures early in the day (O'FARRELL, 1971).

The dissections show that the amount of abdominal fat is moderately well correlated with ovarian stage in *A. junius* but seems unlikely to be a useful indicator of immaturity in *P. flavescens, S. vicinum* or *T. lacerata.* An early need is to determine the endowment of abdominal fat in the newly emerged adult of the main migratory species encountered at Point Pelee, and in particular to compare this endowment in resident and migratory populations of *A. junius* in southern Ontario — an undertaking made feasible in appropriate habitats by the careful work of TROTTIER (1971).

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