

COMMUNAL ROOSTING IN *POTAMARCHA CONGENER* (RAMBUR) AND ITS POSSIBLE FUNCTIONS (ANISOPTERA: LIBELLULIDAE)

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Communal roosting is described at 9 sites all close to a temporary pond on the campus of Madurai Kamaraj University, south India, observed between November, 1987, and the end of January, 1988. Up to 100 males and females, all sexually inactive, were found at one roosting site whereas others normally contained smaller numbers. Some sites were in regular use for at least 70 days. Communally roosting females had immature ovaries whereas males contained apparently mature sperm. Over 400 dragonflies were individually marked and this showed that many of them returned to the same roosting sites for up to at least 23 successive nights. The sites were dead twigs on trees which offered good fields of view. By using pinned, dead individuals and by altering the positions of roosting twigs, evidence was obtained to suggest that the locations of sites are learnt visually and that they do not provide any special microclimatic benefit. The possibility that communal roosting serves an anti-predator function in a species which may remain reproductively inactive throughout a long dry season is considered.

INTRODUCTION

Dragonflies breeding in temporary habitats in areas with seasonal rainfall may survive long dry seasons either as drought-resistant eggs, as larvae buried in damp mud below dried out ponds or streams, or as adults either in a state of delayed sexual maturation or by migrating to wetter regions (CORBET, 1962, 1980, 1984; KUMAR, 1972; WATSON, 1982). GAMBLES (1960) has described the appearance of mature *Lestes virgatus*, *Gynacantha* spp. and *Crocothemis divisa* at the start of the wet season in Nigeria, which have probably survived the long dry season as adults, in some cases becoming sexually mature shortly before the rains start. Thus, whereas in temperate regions larvae tend to be long-lived and adults short-lived (but cf. UEDA & IWASAKI, 1982), in the tropics the reverse may be true for some species breeding in temporary habitats.

Roosting behaviour has been observed in many dragonfly species (FRASER, 1962; PENN, 1950; O'FARRELL, 1971; PARR & PARR, 1974; HASSAN, 1976). FRASER (1944) described aggregations of roosting *Bradinopyga geminata* in India, and GAMBLES (1971) noted associations of *Lestes virgatus* returning to the same roost night after night in Nigeria. Recently, JOSEPH & LAHIRI (1989) described dense aggregations of *Potamarcha congener* roosting in the same branches of *Casuarina* trees night after night during April at Calicut in Kerala, south-west India. However, no attempt has been made to determine the function of communal roosting behaviour or the mechanisms of cluster formation.

An account is given here of observations and experiments carried out on several clusters of roosting *Potamarcha congener* (Rambur) near Madurai in south India, and some suggestions are made about the functions of communal roosting in the context of adult survival of the dry season and the avoidance of predation.

LOCALITY, MATERIAL AND METHODS

Observations were carried out in the vicinity of a small lake in the Botanic Garden of Madurai Kamaraj University in south India ($9^{\circ}58'N$, $78^{\circ}07'E$), between 7th Oct. 1987 and 2nd Feb. 1988. The lake was surrounded by trees on 3 sides and was open on the fourth (Fig 1). A small tree, *Syzygium cumini* (L.) (Myrtaceae), 5-10 m tall, was planted in rows on the west side of the lake, while to the north there were *Casuarina* and various leguminous trees. Monsoon rains in 1987 at Madurai were heavy in October and early November, decreased in late November and ceased after the first week of December. The lake level rose in October, remained high in November, and fell rapidly in

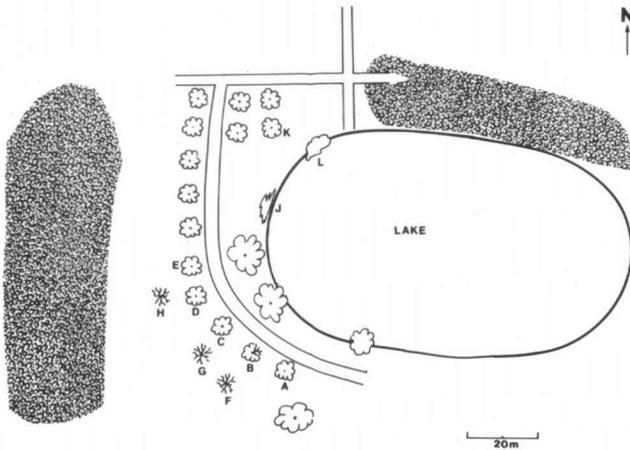


Fig. 1. Sketch map of roost locations A-L, mostly on small trees (*Syzygium cumini*) situated to the west of the lake in the Botanic garden of Madurai Kamaraj University.

December and January, the lake drying out completely by Jan. 19th. The lake is normally dry for 7-8 months of the year.

Thirty-eight males and twelve females of mature *Potamarcha congener* were individually marked on the wings after capture at or near the water between 2 and 21 Nov., using Staedtler Lumocolor permanent markers of several colours. Red marks tended to fade after about 3 weeks and they were therefore re-applied. A further 175 males and 185 females, all sexually inactive, were individually marked between Dec. 21 and Jan. 21st in the vicinity of the *Syzygium* trees where they perched during the day and roosted at night. Marking was carried out either in the morning between 11:00 and 13:00 h (Indian Standard Time), or in late afternoon between 16:30 and 17:30 h. Records were kept of the sex and approximate age of marked individuals and of the time and place of marking. Individuals of *P. congener* commonly remained motionless for several minutes after being released, exhibiting thanatosis, and they could therefore be allowed to recover on the sites on which they had been caught. Most individuals remained in the area after marking for at least a day.

Identifications were facilitated by use of a field monocular. Females were distinguishable at a distance of several metres by the prominent foliations on the 8th abdominal tergite. Analysis of individual positioning and of changes of position were also carried out on 134 photographs of roosting dragonflies. At this latitude the difference between the longest and shortest days is 1.56 h, and the mean change in daylength is approximately 0.26 min per day. Sunrise on Nov. 28th was at 06:18 h and sunset was at 17:54; on Jan. 28, sunrise was at 06:41 and sunset at 18:22 h (I.S.T.).

RESULTS

NOTES ON REPRODUCTIVE BEHAVIOUR

Many *P. congener* were to be found in the vicinity of the lake throughout the 4-month observation period. Immature males and females are black and yellow, whereas mature males develop a blue pruinescence on the thorax which spreads posteriorly to the fourth abdominal segment. Throughout the day many were seen to perch away from the water on the tips of bare twigs or reed stems usually about 1-3 m (exceptionally 4 m) above ground level from where they made occasional feeding flights. At hotter times of the day they perched in the shade or adopted the "obelisk" posture. Competition between individuals of either sex for perches was common.

Sexual activity was observed throughout much of October and in the first half of November at the lake, but thereafter it declined, the last ovipositing female being seen on 8th Dec. However adults continued to be abundant in the vicinity of the lake even after it had totally dried out on Jan. 19th until at least 2nd Feb. when observations ceased.

Sexually active males adopted and defended territories along the lake margins repeatedly returning to the same perch after patrolling flights or encounters with intruders. Of the 38 males marked between 2 and 21 Nov., 12 were observed to be intermittently active on territories for periods of up to 30 days, returning many times to the identical waterside perches.

Many copulations were observed near the water. They took place in the air and lasted 5-10 s. Females oviposited close to the margin by slowly rotating about a

point and vigorously flicking droplets of water, presumed to contain eggs, onto the bank where they landed 10-15 cm above the water level. Parts of the bank with exposed mud seemed to be preferred. Ovipositing females were normally guarded by males. Eggs, dumped by females in the laboratory, were found not to withstand desiccation but would develop without delay if kept moist. Development was completed in 7 days at 28-30° C, but hatching did not occur until the eggs were immersed in water which was in some cases delayed for > 1 month. Eggs would commonly hatch within 5 min of immersion in water deoxygenated by previous boiling, but not at all, or only after a long delay, when placed in water through which air was bubbled. Water plus oxygen shortage may therefore together provide the necessary hatching triggers (P.L. Miller, in prep.). This suggests that, in nature, hatching occurs only when the eggs are submerged and not when they experience heavy rain without being submerged.

ROOSTING SITES

Roosting was seen to occur at the following sites (Fig. 1). All were on small trees of *Syzygium cumini* in the vicinity of the lake, unless otherwise stated:

- (A) A tree 5.04 m in height with 10% of its branches dead; the roost was on the east face and was used temporarily in December.
- (B) A tree 6.0 m in height with 15-20% of its branches dead: B1, a roost on the south-east side of the tree in dead branches facing tree A, used temporarily in December; B2, a roost on the east face of the tree in dead branches 2.5 m above ground, used throughout most of the study period.
- (E) A tree 10 m in height with 35% of its branches dead. There were two sites on dead branches 3-4 m above ground, used temporarily in December.
- (F) A dead tree 6 m in height: F1, a roost on the N.W. side towards tree G, 3 m above ground and used temporarily when the cluster on G was disturbed; F2, a small roost close to the trunk, facing east and 2.2 m above ground, used throughout most of the observation period.
- (G) A dead tree 5.28 m height: G1, a roost on the south side 2.5 m above ground which was used consistently until disturbed on Jan. 12th; G2, a site also on the south side 3 m above ground, used after the disturbance in mid-January.
- (H) A tree about 7 m high, 80% dead. Not used as a roosting site but commonly as a staging post on the way to F, G or B.
- (J) A pile of dead branches of *Bougainvillea* near the lake bank. The roost was 1 m above ground and was used temporarily in January.
- (K) A smaller tree, 2.5 m high and 10% dead. A small site on the east side of the tree was used sporadically in January.
- (L) A small bush of *S. cumini* about 2 m high and growing on the lake bank. The roost site was 1 m above ground on the south side among dead twigs. Over 100 individuals used this roost; it was discovered only late in January although it was probably in use for a long period.

Roosting behaviour was first noted on 25th Nov. and it continued until at least 2nd Feb. when observations ceased. Observations were made mainly on three roost sites, B, F and G, which were in use throughout this period, and on a further 5 sites used intermittently (A, E, J, K, L). All roosting sites (except J) were on the

terminal parts of dead twigs of *Syzygium cumini*. No individual was seen to roost on *Casuarina* trees, although these were common nearby (cf. JOSEPH & LAHIRI, 1989).

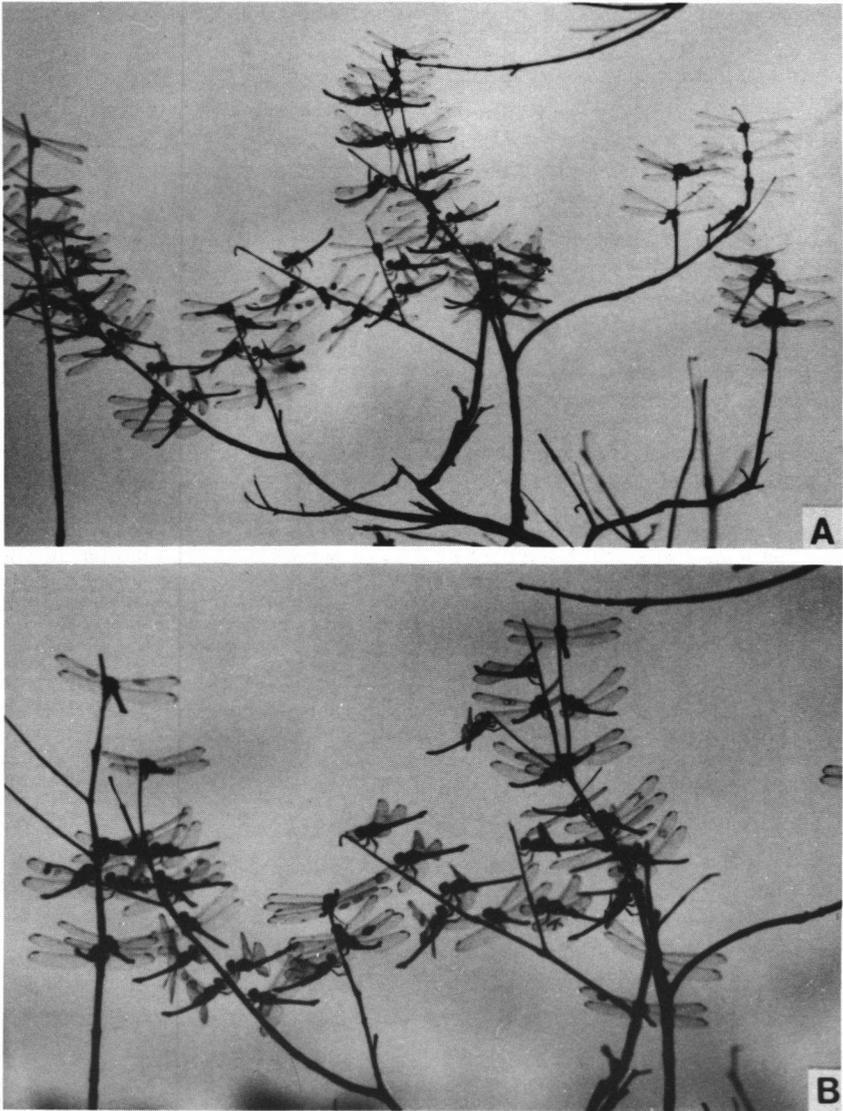


Fig. 2. Two photos of the roost at G taken 15 min after sunset to show that the same twigs were used on different evenings, 6 days apart.

Roost sites were usually 2-2.5 m above the ground, except for *L. Dragonflies* usually assembled in several sub-clusters on the terminal parts of adjacent twigs which formed one roost (Fig. 2). The selected twigs did not face in a consistent direction, were not exposed to late evening or early morning sunshine and did not seem to differ from others in the vicinity: all were leafless and allowed a good field of view.

Fifty-six marked individuals were observed over a 3-week period perching during the mornings within about 20 m of the roosts. On only 12 occasions did one of them join an observed roost. Most of those which did join roosts were not found during the day within 100 m of the roosts, except after 16:00 h. Likewise those which were caught and marked between 16:30 and 17:30 h did commonly join one of the observed roosts later the same day. Although the area may have contained some undiscovered roosting sites, these observations suggest that nocturnal roosting and diurnal feeding sites are normally well separated, as proposed by JOSEPH & LAHIRI (1989).

ROOSTING BEHAVIOUR

About 60 min before sunset many *P. congener* began to gather within 10-20 m of a roost site, perching on surrounding vegetation sometimes within 10 cm of each other. Activity became more intense as the light faded 5 min before sunset, and 2, 3 or 4 individuals were frequently seen to fly round the roost site several times, closely following one another before settling on or near the site. Such "following" behaviour was very characteristic of individuals about to roost. Just before settling they usually hovered above others already perched on the site, and these responded by fluttering the forewings weakly at < 10 Hz (confirmed photographically), a response which appeared to induce settling. When the cluster was well formed, the wing fluttering of 20-30 perched individuals in response to latecomers produced an audible rustling.

As the numbers built up there was much jostling for position and many took off again, flew round and resettled very close to others, sometimes landing on the abdomen of a settled individual; this evoked bending movements of the abdomen until the "intruder" took off. Many pairs settled opposite each other on a twig with their heads separated by only about 5 mm, or they perched immediately above or below one another in tightly packed rows (Figs 2 & 3). In this way 20 or 30 might rapidly assemble along 10 cm of a single twig. The build-up of a cluster was examined in photos taken at ca. 2-5 min intervals (Fig. 4). Twenty min after sunset, activity had almost ceased although a few latecomers continued to arrive for a further 10 min.

Roosting dragonflies perched more or less horizontally or sometimes at an angle according to the orientation of the twig and the proximity of neighbours, but they did not hang vertically (cf. CORBET, 1962, p. 133; HASSAN, 1976),

except in heavy rain. Their wings were held at the midposition or, more usually, slightly elevated. Females commonly held the abdomen flexed dorsally on the thorax by about 60° , with the 9th segment bent upwards further by $25\text{--}30^\circ$, a position which caused the 8th-segment foliations to show prominently. In many males the whole abdomen tended to be curved dorsally (Fig. 5). These positions,

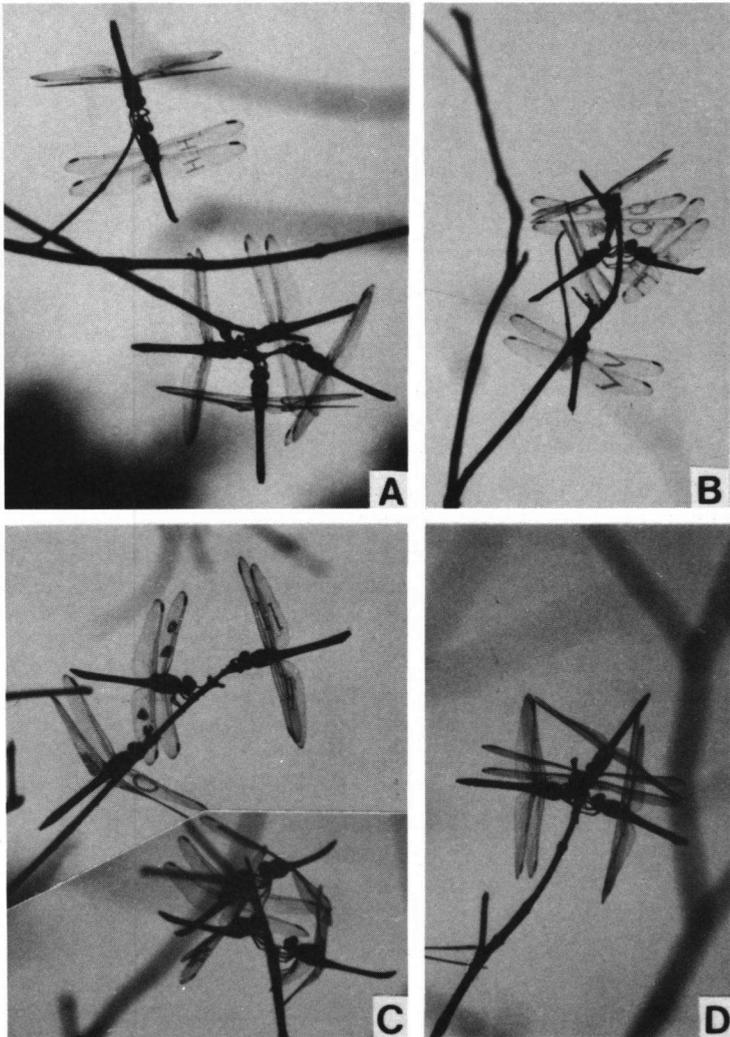


Fig. 3. Photos of twigs in the roosts at B1 and G taken on different evenings. The groups consist mainly of females, but in the lower group in C, 4 males cluster together.

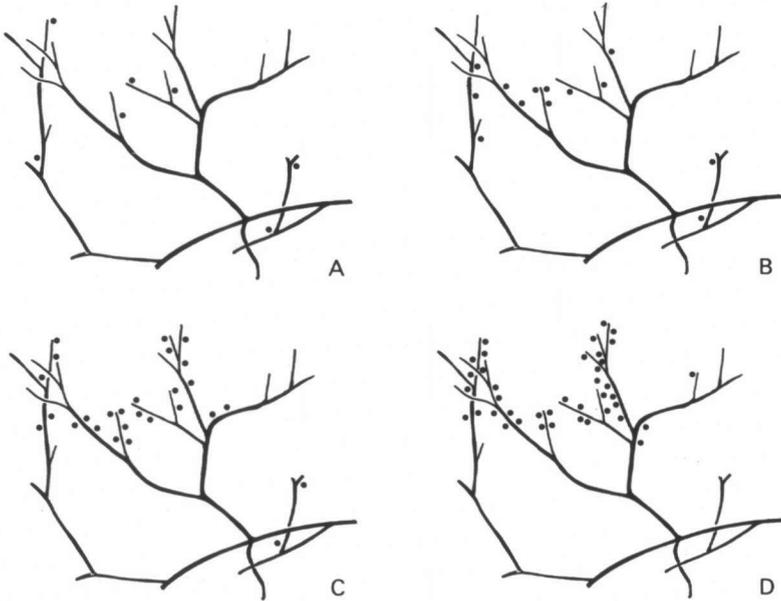


Fig. 4. Diagrams of the roosting twigs at G showing the assembly of roosting dragonflies (spots). The drawings are traced from photos taken at 2-5 min. intervals. A is at sunset. The twigs are the same as those shown in Fig. 2.

which were clearly different in the two sexes, were adopted only after dragonflies had been perched for several minutes. By dawn all held their abdomens straight.

The nightly totals at roosts B and G are given in Figure 6. The marked drop in numbers at roost G after Jan. 12th was caused by the experimental perturbations described below. They caused the group to split into subgroups which roosted nearby, and their totals have been lumped. At sunrise the roosting groups were unchanged. The first activity commenced 40-45 min after sunrise when individuals commenced wing-whirring and flew to perches nearby, the group gradually dispersing.

The roosting sites of up to 59 marked individuals were

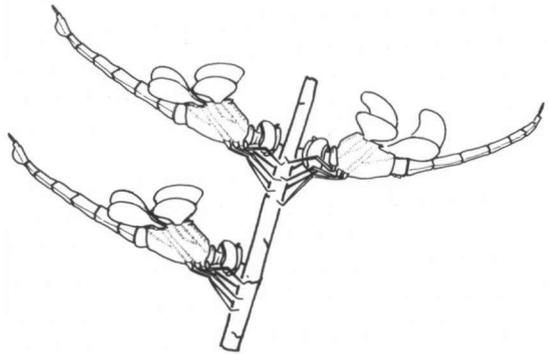


Fig. 5. Drawing of 2 females (left) and one male (right) in their characteristic roosting postures with abdomens elevated.

recorded on 31 nights between December and February, and Table I shows the roosting sites of 22 of them observed during January. During December, individuals could occasionally be found roosting singly, but by the middle of January none was seen outside the clusters and many rejoined the same roost night after night, although not necessarily perching on the same twig (e.g. males Nos 196 & 299; females Nos 284, 329 & 335 in Tab. I). However a few individuals were less consistent with respect to the roosting site (e.g. male No. 229 and females No. 211 in Tab I). No individual was observed to roost communally for more than 23 days although roosts B and G were in constant use for at least 70 days.

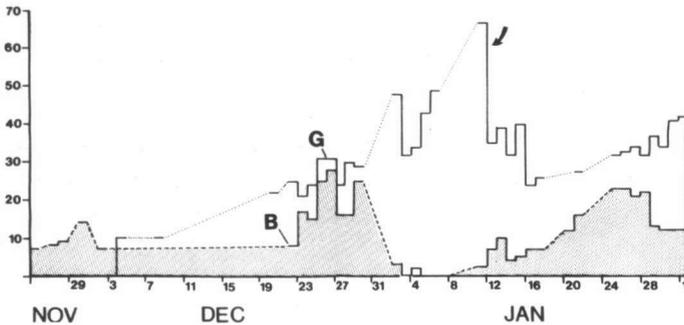


Fig. 6. The total numbers of dragonflies roosting on successive evenings at site B1 (hatched) between Nov. 27th, 1987, and Feb. 1st, 1988, and at site G between Dec. 4th and Feb. 1st, 1988. Note the temporary abandonment of B1. — [The arrow on the G records indicates the time when there were experimental disturbances of the site (see text). — Days when no record was made are indicated by dotted or dashed lines].

SEX RATIO

The sex ratio among those caught and marked in the vicinity of the roost sites was close to 1:1, there being 51.5% females in a total of 361 individuals. However the sex ratio in some roosts was biased: at G, sampled for 14 nights, 81% were females out of a total of 552; at B, sampled on 10 nights, 37% were females out of a total of 100; at F, sampled on 14 nights, 45% were females out of a total of 71. Thus at G, females were more numerous, but at F and B, males tended to predominate. The samples are too few to measure a possible relationship between group size and sex ratio.

Closely perched pairs, as well as triplets and quartets which perched face-to-face on either side of a twig, might contain one or both sexes (Fig. 4). Thus roosting behaviour did not seem to be different in the two sexes or in small and large groups.

STATE OF MATURITY

Individuals were gauged to be teneral when their cuticle was soft, their wings glittered and their flight was relatively weak. Teneral individuals were found commonly in November and December, but thereafter there were few, and none was found after 12 Jan. Of 193 adults caught between 21 and 29 Dec., 16% were teneral, but among 132 caught between 3 and 12 Jan., only 4% were teneral.

Twenty unmarked females were caught at a communal roost on Feb. 2nd. Dissection showed that in all, the ovaries were immature, the follicles being of a uniform small size, corresponding to CORBET's (1984) stage I. None contained sperm in the bursa or spermathecae. Examination of females, marked as post-ternerals, showed that their gonads remained immature for at least 26 days after marking. Of 10 immature males (i.e. those with no pruinescence) all had their primary reservoirs full of apparently mature sperm, and some sperm was detected also in their vasa deferentia. Their testes were well formed containing distinct spermatogonia. No sperm was found in the secondary genitalia. In contrast all 10 non-roosting mature males (with blue pruinosity) examined in November contained in addition much sperm in the sperm vesicle of the secondary genitalia. Thus although communally roosting *P. congener* were sexually inactive, the males had well developed gonads. Both sexes had abundant fat deposits and well-filled guts. Mature males with blue pruinescence did not roost communally, although a few were to be seen in the vicinity of the lake in December and occasionally in the first half of January.

EXPERIMENTAL DISTURBANCES

Roosting clusters at dusk and dawn were extremely alert and were more easily disturbed than were single individuals perched during the day. When a cluster was disturbed it usually soon reformed on the same site. However, when strongly disturbed 30 min after sunset by hitting the branches with a stick, the cluster did not reform there on that night or on the following one, although some individuals did join a neighbouring roost. This operation was carried out twice and involved 62 dragonflies. Clusters were equally easily disturbed around sunrise but the clusters did not then reform. Individuals could fly off instantly at an air temperature of 20° C, although they normally preferred to wing-whirr before take-off at this temperature.

To explore the means used by *P. congener* to return to the same roosting sites night after night, the roosting branch on tree G was cut off and taped at the same height but in a new position 1 m away. Another branch of the same size but slightly different in shape was then taped where the original branch had been (Fig. 7A, B). For about fifteen minutes near sunset many individuals flew around the new branch and several settled on it momentarily but then took off again. None

visited the original branch. Eventually a cluster of about 60 settled on a branch of tree F, 0.75 m from the new branch, a site which had not been used previously. This cluster was then disturbed and after a few min, 25 resettled on the same branch and a further 10 did so on a nearby branch on G where they remained for the night (Fig. 7B). Thus no individual roosted on the original branch in its new position or on the replacement branch, although the site had before been used nightly by up to 70 individuals.

The next day the old branch on tree G was taped back exactly in its original position. The following evening 39 dragonflies roosted on it and both new sites, adopted on the previous evening, were abandoned (Fig. 7C).

In order to test the effects of small changes of position of the selected branch, a long stick was attached to it with which it could be extended towards tree F. When the branch was extended by 60 cm, many individuals flew repeatedly round it with some perching temporarily on it, but none remained. A cluster of 16 formed on a neighbouring branch of G, and two clusters, of 7 and 9, formed nearby on tree F, all being within 2 m of the original site (Fig. 7D). The following day the experimental branch was returned to its original position, but only 6 dragonflies chose to roost on it while 18 roosted nearby on G and 16 on F. Further manipulation of the experimental branch soon caused all dragonflies to abandon it, 40 of them adopting a new roost on G, only 0.5 m from the experimental branch, which was then used consistently until observations ceased 2 weeks later.

To investigate the possibility that perched dragonflies might attract others to settle nearby, a group of 3 male and 4 female dead *P. congener* was pinned to a

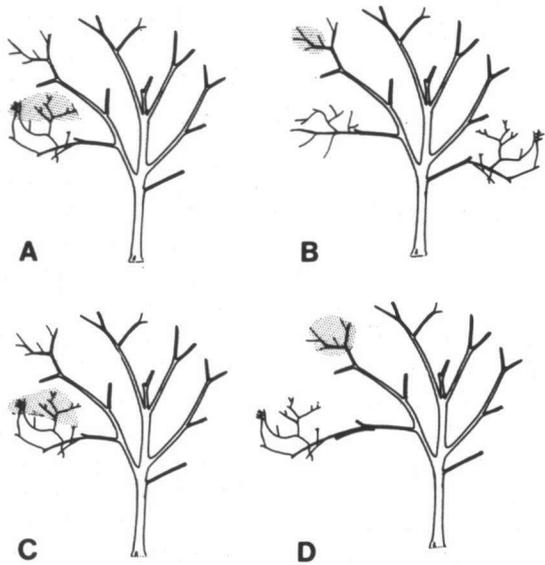


Fig. 7. Summary of some experiments on the effects of roost disturbance. Hatched areas represent roost sites: (A) roosting cluster at the normal site on G; — (B) the exchange of the roost branch with another caused the roost to form on a new branch above the position of the original roost; — (C) on the following day, after return of the original roost branch, the roost again formed on the original branch; — (D) the roosting branch was protruded slightly and the roost formed on the new branch above it as in B.

twig in a roosting posture 0.5 m from the branch which was being utilised as a roost on G. At sunset many arriving dragonflies hovered over the dead individuals but then flew on to their normal roost. Perched, motionless dragonflies did not therefore evoke settling, perhaps because they failed to provide appropriate visual (wing fluttering) or chemical (pheromonal) signals.

DISCUSSION

On the campus of Madurai Kamaraj University during December and January large numbers of individually marked male and female *P. congener* were observed to return to the same sites night after night to roost. The selected sites were on dead twigs of a small tree, *Syzygium cumini*. Roosting females were sexually immature, but males although immature in colouring and sexually inactive contained well developed gonads and had well-filled sperm reservoirs. Declining light intensity seemed to initiate roosting behaviour which occurred earlier on overcast evenings (cf. PENN, 1950). Two questions concerning communal roosting merit discussion: how it is achieved and what its adaptive value is.

With regard to the first question, two hypotheses can be considered: the earliest dragonflies to arrive may either respond separately each evening to locally optimal microclimatic conditions, or they may return to a previously visited locality, recognised on the basis of chemical or visual information. In either case those arriving later may respond to the presence and signalling of the first-comers. Although the trees offered many dead twigs with a similar orientation and at the same height, only a few were used consistently. Moreover the willingness of the dragonflies to abandon one site after it was disturbed and select a new one nearby suggested that the original site had no greatly preferred microclimatic feature and that the initial choice of twigs was to some extent arbitrary, provided it met certain requirements (e.g. good field of view).

Chemical and visual signals could both be involved in the recognition of a site and the presence of other dragonflies. JOSEPH & LAHIRI (1989) suggested that *P. congener* might aggregate as a result of the release of a short-duration pheromone by the first arrivals. They also suggested that a long-duration marker pheromone might allow individuals to identify the same twigs on successive evenings. The abdominal flexing and wing fluttering described in roosting *P. congener* are similar to movements associated with pheromone release in moths (CONNER & BEST, 1988). However, dragonflies are not known to release pheromones, have only small numbers of chemoreceptors on the antennae (SLIFER & SEKHON, 1972) and are thought not to possess appropriate glands. Moreover if pheromones were present in *P. congener*, they might be expected to be used also by other members of the family, though possibly with different functions as in Noctuidae (SPANGLER, 1988). In addition a persistent pheromone should have allowed individuals to locate the same branch after it had

been moved a short distance, but this was found not to be the case. Better experiments would have involved the substitution of a branch of identical shape, or the washing of the roost twigs to remove any pheromone, but these were not attempted. At present the contribution of a pheromone cannot be ruled out but seems unlikely.

It seems more probable therefore that the repeated use of the same roost depends on a good visual memory. This accords with other features of dragonflies such as their acute vision and the possible use of memory to return to the same territories on successive days. Wing fluttering and abdomen curving could then be visual signals, as they are in some other species, e.g. in *Palpopleura l. lucia* which uses wing fluttering to deter conspecifics from roosting nearby (HASSAN, 1976). That they are responding to each other visually is also suggested by their gathering in the area an hour or more before sunset and by the characteristic "following" behaviour seen at the time of roosting.

Some of the same roosting sites were used throughout the 70 days of observations but no marked individual used a site for more than 23 days. Thus within the population, a "tradition" for the use of particular sites was maintained, perhaps by dragonflies learning from one another. That learning may be involved is also suggested by the observation of the temporary abandonment of and subsequent return to roost B (Fig. 6).

The second question concerns the function of communal roosting. It seems unlikely that the observed clusters were dense enough to provide any microclimatic or thermoregulatory benefit, suggestions made to account for clustering in some other insects. Two hypotheses may therefore be considered: clustering may promote long-term cohesion of the group, or it may enhance predator-avoidance.

If communal roosting fostered group cohesion in a population of dragonflies this might ultimately confer some mating benefit. By staying together in a state of reproductive diapause near where they had emerged throughout a long dry season, breeding might be facilitated as soon as the rains returned (cf. GAMBLES, 1960). On the campus, *P. congener* would probably have no opportunity to breed between December and the following August or September, unless they changed their habitat preference, or emigrated. In the Dehra Dun Valley of northern India, *P. congener* is univoltine and its flight period lasts from mid-June to the end of September (KUMAR, 1972). It oviposits in temporary ponds in July and teneral adults are first seen in August and September. These observations suggest that adults either emigrate to other parts or remain for a long period in forest nearby until the following summer, although they have not been seen elsewhere during the winter months (PETERS, 1981).

Communal roosting could alternatively be seen as a preparation for gregarious emigration, a suggestion supported by the large quantity of stored fat found in individuals (cf. CORBET, 1984). However, *P. congener* is not known to be

migratory although a few were once reported to be flying about 110 km off the coast of Sri Lanka (British Museum specimens: October, 1930).

JOSEPH & LAHIRI (1989) considered that communally roosting dragonflies benefitted from greater vigilance, thereby reducing predation. If one individual detected a predator, its response might alert others. At dusk, clusters of dragonflies were found to be very wary and all would sometimes take off in response to movements of the observer 3-4 m away. Perching on the tips of dead twigs may give good all-round vision and help them to avoid nocturnal predators which climb on the trees such as geckoes and tailor ants (*Oecophylla smaragdina*), both of which were very abundant on living trees in the vicinity. Tailor ants were seen to catch any dragonflies (*Pantala flavescens*, *Tholymis tillarga*) and other insects which came to lights. Communal roosting may therefore represent "selfish herd" behaviour in which each individual benefits by perching as near the twig tip as possible, at the same time gaining from the presence of others which give an early warning of predators. For example the fluttering of a dragonfly caught by ants would probably cause others nearby to take flight. The abandonment of a roost after it had been disturbed during the experiments reported here also supports the anti-predator hypothesis.

In conclusion, therefore, it seems likely that communal roosting in *P. congener* serves to reduce nocturnal predation, and that this enhances survival in a long-lived species which may remain in reproductive diapause throughout a long dry season.

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