

**PHILOPATRY, HOMING
AND DISPERSAL IN *LESTES BARBARUS* (FABRICIUS)
(ZYGOPTERA: LESTIDAE)**

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Field experiments at Castel Porziano, Rome, Italy, have shown that *L. barbarus* populations are highly philopatric, their return to their native ponds being based on homing behaviour. Some ponds lacking any *barbarus* may prove suitable for larval growth up to emergence, but precocious drying up would often cause the extinction of larvae. Short-range dispersal is so scarce that colonization of non-populated ponds is not promptly obtained.

INTRODUCTION

The present study was carried out in 1975 at Castel Porziano (Rome), where *L. barbarus* populates temporary ponds that in summer dry out for a long period.

At those ponds, *L. barbarus* breeds from the beginning of August up to the first half of October, but a few individuals may attend the ponds up to the end of October. Eggs undergo diapause (cf. also AGUESSE, 1968, pp. 27, 77) and hatch in February (G. Carchini, unpublished). Emergence takes place between the second half of May and the first half of June, when the ponds start drying up.

At Castel Porziano, *L. barbarus* does not colonize all the available ponds, though the non-populated ponds appear to be similar to the populated ones at least in size (ca 25-50 m diameter) and in the vegetation where eggs are inserted (UTZERI et al., 1976). At the ponds inhabited by *L. barbarus* it is possible to find the imagines within the first seven days after emergence and in the reproductive season, while between the complete drying up of the ponds and the beginning of the reproductive season no adults were noticed there (cf. also UTZERI et al., 1976).

AGUESSE (1960) found marked *L. barbarus* individuals 2 km away from the site where they had emerged, but we did not have any indication of individuals of our populations actually behaving similarly. In fact, our insects could have spent their maturation period in shrubs or trees close to the ponds from which they had emerged. We were not able to check either of these two alternatives, because the bush around the ponds was quite impenetrable.

The study aimed to increase our knowledge of *L. barbarus* pre-reproductive biology, providing an answer to the following questions: is philopatry in *L. barbarus* as strict as it appeared to be from our preliminary work (UTZERI et al., 1976), or is there some dispersal; and if there is, why does the species not colonize the non-populated ponds; are these ponds, even though they resemble the populated ones, ecologically inadequate for larval growth, and is the absence of any population due to factors other than not being chosen as a mating place by sexually mature individuals; do the imagines spread out in the reproductive period to a certain distance from the ponds from which they emerged as reported by AGUESSE (1960), and in this case, if experimentally displaced, are they able to return to their original habitats.

METHODS

Adults were netted and marked with conspicuous enamel colour spots on the wings, according to CONSIGLIO, ARGANO & BOITANI's (1974) code, so they would be easily distinguishable in the field, and would have scarce chances of escaping recapture.

Larvae were translocated by means of plastic bottles containing pond water, and imagines in wood, wire mesh and glass cages measuring 26x26x28 cm. During translocation these were put in the boot of a car, in order to prevent the insects from having the sight of the landscape and/or the sun. In all cases, transfer and releasing of the insects were carried out on the same day when capture and marking had been made, and as quickly as possible, to avoid harming the insects.

The release of the marked insects was effected by putting the opened cages on the ground, each sample in the place that had been chosen for a particular purpose. In case of control sample the dragonflies were released at the marking place just after marking. As soon as released, the marked insects were kept under observation until they took flight, and only those that appeared to have incurred no harm from netting and marking operations were recorded on the marking book.

All individuals belonging to a sample got the same pond-specific mark. In the days when we could gather a consistent number of insects, marking operations for each sample took place within a single day. Thus, these marks are also date-specific. With some samples, two days were needed for netting and marking, and the same pond-specific mark was also used in these instances (Tabs I, II). We assumed that the insects that were captured at a particular pond either in the emergence or reproductive period, had emerged from that pond which will be referred to, in the following, as to their "home" or "native" pond. With the mature individuals, we assumed as their home pond the pond at which they were netted, in accordance with the results of our previous work (UTZERI et al., 1976) from which we obtained the indication that imagines do not undergo dispersal (0% dispersal rate in two samples from different populations). During the reproductive period, when recapture took place, the recaptured insects got a second colour spot, that was also pond-specific, and the number of recaptured insects and their localization were annotated daily.

The age of young individuals was determined on the basis of the colour of the pterostigma, which

is whitish in the first days following emergence, but turns into white and brown after about 4 days. Looking day by day at insects marked on the day of emergence, we could know that the dragonflies showing a whitish pterostigma were 0 to 4 days old, while those with white-and-brown pterostigma were older than 4 days. Taking into account the dates on which the first emergences had been recorded at a particular pond, we could also estimate the maximum age of these latter individuals as not exceeding ten days.

In the reproductive period the marked insects were searched for at the ponds they had been marked and/or released, as we expected to find them there, as well as at all the water bodies nearby. In the homing experiments we considered as actually homed only those individuals that could be recaptured at the pond area.

Two to four persons worked in the field on 25 of the 50 days during which recapture was performed. On each day of presence, the observers were in the field from 1100 to 1600, covering the period of *L. barbarus* maximum daily activity. During this time, the ponds were inspected almost continuously, each one at least every 20 minutes.

In the following, we will refer to the adults managed by us in the emergence period, as to the young imagines, while to those in the reproductive period, as to mature imagines.

The samples of mature individuals that were displaced for the homing experiments were formed by male insects, because in the reproductive period we were not able to gather a consistent number of non-mated females. We did not utilize females from tandems, as they could have copulated already, and we were not sure whether the drive to lay eggs, that usually is shown by *L. barbarus* with oviposition closely following copulation, would have led inseminated females to stop at any suitable place, thus disturbing a possible drive to return home.

For the experiments on philopatry, we also utilized ponds void of any *L. barbarus* population. In these ponds, that were visited by us quite regularly during a 3-years investigation (including the summer when the research was made) we could never find either larvae or young and mature imagines. The absence of larvae was checked by means of monthly dredging of the pond bottom and vegetation with a dredge-net. Dredging was also made immediately before putting the larvae into the pond and two days later, and larvae were taken only in the latter instance. During the reproductive season, we listed all the individuals whose localization indicated that they surely or presumably had undergone dispersal. We considered as surely dispersed the marked individuals that were found at other ponds than those where they had been marked and/or released, and as presumably dispersed the unmarked ones, of which we did not know the emergence pond, but which were found at ponds known as void of any autochthonous population.

PHILOPATRY

EXPERIMENTAL SET-UP

A larval sample, consisting of 236 specimens in the last two instars, and another one of 188 imagines, taken in the emergence period, was introduced into two ponds void of any autochthonous population. We intended to discover if the pond into which the larvae were being put would have permitted their survival until emergence, and if the young taken to a host pond would use this as a mating place. Also, since the imaginal sample was divided into two age groups (see below) it would have been possible — in case the younger specimens had been recovered in a different rate than the older ones — to determine at which age the bond with the individual's pond of origin (in this case the host pond) is formed.

The larvae were taken from pond T20 to pond T36 (cf. Fig. 1). A large number of them underwent emergence between May 22nd and June 3rd. The imagines were not marked. Starting August 7th, up to September 26th a conspicuous number of mature individuals were seen at pond T36 performing

reproductive activities.

The adult sample was translocated from pond T35 to T10 (cf. Fig. 1). This sample, consisting of males and females, was divided into two age groups: 91 individuals, not older than 4 days (whitish pterostigma), were marked R5, and 97, between 4 and 10 days old, were marked R6.

A few days after this sample had been translocated, another sample of young imagines was marked and released at pond T1. This consisted of 124 male and female individuals, that got the marks B5 (39) and B6 (85), in accordance with the same criteria as for the sample R5 + R6.

During the reproductive period, at pond T10 7.7% R5 and 23.7% R6 individuals were recaptured. At pond T1, 10.25% B5 and 30.6% B6. At nearby ponds we found 1 R5 and 1 R6 individuals (total 1.1%), and 0 from samples B5 and B6. These data are gathered in Table I.

DISCUSSION

Pond T36, into which the larval population had been introduced, proved to be adequate both for growth and emergence of the larvae and as a mating place. We think improbable that those individuals that gathered at that pond for mating had emerged from other ponds than T36, as pond T36 had been recorded void of any larval and adult population up to that year. Moreover, since larvae had been put into it some months earlier, it would have been at least an unlikely coincidence. Thus, the result of this experiment may also give an indication about the philopatry of that population.

It was interesting to put on record the strict localization of mature individuals

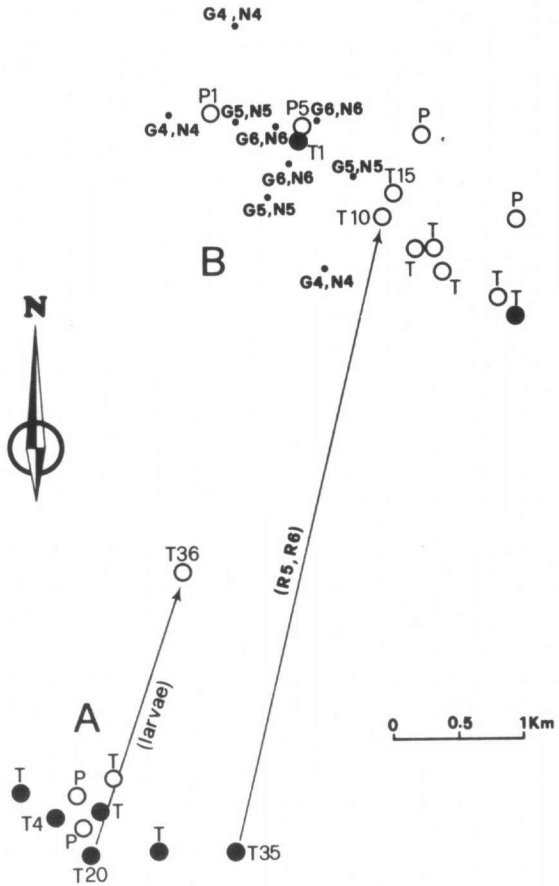


Fig. 1. The research area (lat. 41° 40'N; lon. 12° 20'E): ponds in black were inhabited by *L. barbarus* in 1975; white ones were not. Distances between ponds are to scale; pond dimensions are not. Dots indicate the sites where samples displaced for the homing experiments were released. The marking codes of the samples concerned are reported close to each dot. P and T indicate permanent and temporary ponds respectively.

in the area of the pond. In fact, just 30 to 50 m away, there was a depression in the ground that formed a typical temporary pond, richly supplied with reeds that are commonly utilized by *L. barbarus* for oviposition. Even so, in the course of many inspections, no individuals were ever seen in this area right next to pond T36.

Table I

Marking-recapture data for young imagines (R5, R6) taken from pond T35 into pond T10 and (B5, B6) released at pond T1, which they emerged from (No. days = number of days actually needed for marking and recapture operations)

| Pond | Marking | | No. days | No. indiv. | Recapture | | | |
|---------------------|---------|---------|----------|------------|--------------|----------|------------|-------|
| | Mark | Dates | | | Dates | No. days | No. indiv. | % |
| T35 → T10 | R5 | 16.V | 1 | 91 | 4.VIII-23.IX | 25 | 7 | 7.7 |
| T35 → T10 | R6 | 16.V | 1 | 97 | 4.VIII-23.IX | 25 | 23 | 23.7 |
| T1 | B5 | 27.V | 1 | 39 | 4.VIII-23.IX | 25 | 4 | 10.25 |
| T1 | B6 | 23-27.V | 2 | 85 | 4.VIII-23.IX | 25 | 26 | 30.6 |
| Others, near T10 | | | | | 4.VIII-23.IX | 25 | 2 | 1.1 |
| Others, near T1 | | | | | 4.VIII-23.IX | 25 | 0 | 0.0 |

} 16
} 24.2

The new larval population survived until the next year, but just as the first tenerals were appearing the pond dried up, preventing us from establishing the size of the surviving population and studying its steadiness in the subsequent years. Even so, we believe that this pond, until then void of any population, could be suitable for *L. barbarus*, if it were not for the fact that, in some years, precocious drying up would have prevented emergence.

Young imagines introduced into pond T10, returned to that pond for breeding after maturation. In 1974 we also could recapture some individuals of a small sample obtained from larvae that had emerged in the laboratory, at a pond where they had been released (UTZERI et al., 1976), but the difficulty of obtaining a consistent sample from the laboratory made those results unreliable.

The almost total absence of marked individuals at ponds nearby that from which they had emerged confirms previously obtained results (UTZERI et al., 1976). We have no indications as to what happened to non-recaptured individuals. We have no idea of whether any long range dispersal may have taken place, whereas short range dispersal (among the ponds) was negligible and exclusive of the translocated sample (R5 + R6). During the reproductive period, in 1974 and 1975, not a single individual of a total of 461 belonging to three samples was found anywhere else than at the ponds from which they had emerged, and where they were marked and immediately released while still young.

The overall recapture percent of the host pond samples (16), and that of the samples released at the marking pond (24.2), are comparable to those obtained in previous capture-marking-release-recapture experiments (UTZERI et al., 1976). The difference in the recapture frequencies of each samples do not yield significant values with the χ^2 test.

The recapture frequencies of the individuals less than 4 days old (R5, B5) give significant values in the χ^2 test in respect to those of the elder insects (R6, B6) ($p < 0.01$ and $p < 0.05$, resp).

Temporary ponds have different water cycles in relation to seasonal rain variation and soil structure. (permeability, depth of impermeable strata, etc.). Differences in the soil may cause variations in the water cycle of ponds in a restricted area, even among ponds very close to each other. In our area, for example, the dates of drying up of the astatic basins in 1974 were spread out from May 30th to July 30th, and in 1975 from May 25th to June 30th. Even the water cycle of the single ponds may undergo variations from year to year: pond T1, for example, in 1974 dried up on June 15th, in 1975 on June 25th, in 1977 on May 5th(!), and from 1978 to 1980 around June 30th; pond T4 in 1974 dried up on May 30th, in 1975 on June 25th, in 1977 on May 5th (!), and from 1978 to 1980 between May 30th and June 30th. Therefore, the same pond in certain years may have a water cycle suited for larval growth until emergence, in other years it may prove inadequate, thereby causing the extinction of its population, as happened in 1977 in the case of ponds T1 and T4. Nevertheless, given such variable general conditions, temporary ponds with a rather regular water cycle throughout long periods are functionally very similar to a permanent and isolated habitat, and the regularity of their cycle could act as a selective factor of philopatric behaviour. Even so, in particular years, as we have seen, ponds with normally regular cycle can undergo variations that turn out to be catastrophic for the resident populations. But in spite of this, it could be that the occasional extinction of a single pond population in the whole is of less harm to the species than the sure and continuous loss of eggs laid by dispersed individuals at ponds with inadequate water cycles, as would occur if the choice of the reproductive habitat were not regulated by philopatry.

LENGTH OF MATURATION PERIOD

It is possible to make a rough estimate of the length of the maturation period for the sample B5 + B6, from the time elapsed between the marking and recapture dates of each individual, by adding 2 and 7 days respectively to the marking-recapture interval of the adults marked B5, aged 0-4 days at the marking, and B6, aged 4-10 days. (We roughly assume 10 days as the maximum age for these individuals, as early emergence had already been observed around May 20th, at pond T1, as is reported in the section on methods. For marking dates cf. Tab. I).

The time elapsed between emergence and the beginning of the reproductive period, i.e. the maturation period, averages 98 days ($n=30$; $r=78-128$). The number of individuals recaptured on the various dates is greatly dispersed over the entire recapture period, with the highest frequency (5 individuals) on the 81st and 102nd days.

This value is one of the highest reported for lestids. For *L. sponsa* CORBET (1956) gives 16 days, while ITO & EDA (1977) and UÉDA (1978) recorded 40 and 20-130 days resp. for the same species. For *L. disjunctus* SAWCHYN & GILLOTT (1974b) estimated 16-18 days, LAPLANTE (1975) 27 days and BICK & BICK (1961, *L.d. australis*) 13 days. For *L. congener* SAWCHYN & GILLOTT (1974a) give about 21 days, and LAPLANTE (1975) 15. For *L. rectangularis* GOWER & KORMONDY (1963) report 12-18 days. LOIBL (1958) gives 3 weeks for *L. dryas*, and roughly 15 days for the other European *Lestes*, including *L. barbarus*. LAPLANTE (1975), finally, recorded 22 days for *L. unguiculatus* and GAMBLES (1960; 1976) 6-7 months for several African species.

With references to *L. barbarus*, on the basis of LOIBL's (1958) and our data, one could speculate whether the length of its pre-reproductive period would show a latitudinal cline, thus resembling *L. sponsa* (UÉDA, 1978). CORBET (1980) suggests that the function of a prolonged pre-reproductive period in both species at the lowest parts of their ranges may be the same.

HOMING

EXPERIMENTAL SET-UP

The following experiment was set up to test the imagines' capability of returning from certain distances to the pond from which they had emerged.

In the reproductive period, three samples of mature individuals were marked and released at varying distances from the pond where they had been captured (T1). This was done according to the following standard: 37 individuals marked N6, 200 m away from the pond, 45 marked N5, 500 m away, and 57 marked N4, 1000 m away.

Three other samples of newly emerged individuals with coloured pterostigma had already been marked G6, G5 and G4, and similarly released 200 m (59 individuals), 500 m (59 individuals) and 1000 m (65 individuals) away from their native pond T1.

Each one of the marked samples, both the younger and the elder ones, was divided into three groups, and released at three different sites at the same distance. These sites were chosen the same for teneral and mature samples. (Fig. 1).

A control sample for mature adults, consisting of 31 individuals, was marked N2 and released at pond T1. Sample B6, already used for the experiment on philopatry, was used as a control for the young imagines samples as discussed in the previous section.

Eight individuals marked G6 and 5 N6 were recovered from 200 m, 1 G5 and 5 N5 from 500 m, and none of either sample from 1000 m, but 1 individual of the mature sample N4 was found at less than 100 m from its native pond (see below); 26 individuals (30.6%) of the control sample for the young imagines, and 18 (58%) of the control related to the elder group, were also recaptured (Tab. II).

The time elapsed between the marking and recapture dates for individuals of the same samples

marked when young was $\bar{x}=87$ days for sample G6, 92 days for the single individual of sample G5, and $\bar{x}=90.4$ days for the control sample B6.

Table II

Marking-displacement-recapture data for young (G6, G5, G4) and mature (N6, N5, N4) imagines and for their controls (B6, N2) (In round brackets data for 1 individual recorded near the reference pond but not in the recapture area; cf. the text). In square brackets data referring to control samples. No. days = the same as in Table I

| Mark | Marking | | No. | | Dates | Recapture | | | Recaptured/ expected No. indiv. (%) |
|------|---------------------------|------------|------|--------|---------------|-------------|---------------|------------------------|---|
| | Releasing distance (m) | Dates | days | indiv. | | No. days | No. indiv. | Expected No. indiv. | |
| G6 | 200 | 27.V | 1 | 59 | 4.VIII-24.IX | 26 | 8 | 18 | 44.4 |
| G5 | 500 | 28.V | 1 | 59 | 4.VIII-24.IX | 26 | 1 | 18 | 5.6 |
| G4 | 1000 | 30.V | 1 | 65 | 4.VIII-26.IX | 26 | 0 | 20 | 0.0 |
| B6 | 0 | 23-27.V | 2 | 85 | 4.VIII-24.IX | 26 | 26 | — | [30.6] |
| N6 | 200 | 6- 7.VIII | 2 | 37 | 7.VIII-24.IX | 24 | 5 | 16 | 31.2 |
| N5 | 500 | 8-11.VIII | 2 | 45 | 11.VIII-24.IX | 22 | 5 | 22 | 23.8 |
| N4 | 1000 | 11-13.VIII | 2 | 57 | 18.VIII-24.IX | 21 | (1) | 32 | (3.1) |
| N2 | 0 | 18-19.VIII | 2 | 31 | 19.VIII-24.IX | 20 | 18 | — | [58.0] |

DISCUSSION

The recapture rates of the displaced samples of both young and mature individuals are lower than those of their controls. These differences are obviously due to the experimental conditions.

The lower number of recaptured individuals compared to the marked ones is usually attributed to three main factors: mortality, dispersal and avoidance of recapture. Assuming mortality to be time-dependent, and the average return times being rather similar for the samples of young displaced individuals and their controls (cf. above), mortality has probably affected all these groups in the same degree.

Given the limited size of the pond (30x30 m) the conspicuous colour spots with which the insects were marked, and the amount of time the observers spent at the pond each day, we do not believe that any individuals could have avoided recapture. No spontaneous dispersal was recorded for the control sample B6 (young) (cf. Tab.I), therefore differences between the recapture rates of the displaced samples and of their control are to be completely attributed to displacement-induced dispersal.

If we compute the recapture rates of the young displaced samples in % of that of the control, we obtain 44.4% for the sample displaced to 200 m, and 5.6% for that displaced to 500 m. We consider improbable that orientation by sun was involved in their way home, as during translocation the insects were not allowed to see the sun. Thus, at the time when displaced, the young imagines might have

been acquainted in a certain degree with the area surrounding their pond.

The control sample for the insects displaced in the reproductive season showed a 42% loss over a period of 36 days, from August 19th to September 24th, that is, a 1.2% loss per day. Computing for each displaced sample the individuals loss based on this daily loss and on the number of days passed from the day after marking to the last recapture day, we obtain an expected number of 16 returned individuals from 200 m (37 individuals — 1.2%/day x 48 days x 37 individuals : 100), 21 individuals from 500 m (45 — 1.2 x 44 x 45 : 100) and 32 from 1000 m (57 — 1.2 x 37 x 57 : 100). In respect to these values, the number of individuals actually homed from 200 m represent 31.2% of the sample (5/16), from 500 m 23.8% (5/21) and, with a certain approximation, presuming that also the individuals marked N4 and found less than 100 m from its home pond (cf. above) would have returned home, from 1000 m 3.1% (1/32). From these values it can be supposed that the radius of the area overflowed in the pre-reproductive period may reach 1000 m, though no individuals have been recaptured from this distance at the restricted area of the pond.

Homing rates, not very dissimilar between 200 and 500 m, could indicate that individuals displaced when mature have similar homing capability from points at different distances, within the overflowed area. The relatively low recapture rates and the slight homing frequency decrease with increasing distances, could be in part correlated with individuals stopping at sites where stimuli eliciting reproductive behaviour were perceived, e.g. ponds or crowded populations of its species met during the homing flight. As a matter of fact, a number of individuals displaced when mature, stopped at other ponds than that from which they had been displaced.

DISPERSAL

FIELD DATA

During the reproductive season we recorded 33 dispersed individuals, 13 of which unmarked and 20 marked. Eleven of the 13 unmarked ones were recorded at pond T10, in a ratio of 8 females : 2 males : 1 non-registered sex. Eighteen of the marked individuals belonged to the samples displaced for the homing experiments; 4 of these were from the samples displaced when young, and 14 when mature. The other 2 belonged to the young sample introduced into the host pond T10.

DISCUSSION

We consider the 11 unmarked individuals recorded at pond T10 as dispersed, because that pond had been registered up to that year as non-populated. Literature data show a greater tendency for females to disperse in respect to males (MOORE, 1954; BICK & BICK, 1961, 1968). Basing on this, one could expect that if a number of dispersed individuals would run into a non-populated pond,

there would be more females than males among them. The sex ratio of the few unmarked individuals that we recorded as dispersed is in agreement with this.

Concerning the dispersed individuals belonging to the samples displaced for the homing experiments, probably those displaced when young (4) individuals ran into the pond at which they were recorded a few days after displacement, and took it as their homing goal at the end of maturation, in the same way as the individuals introduced into pond T10 did, while the latter (14), already mature at the time of displacement, probably stopped at the first pond which they ran into, which happened to be a permanent one (P1), provided with suitable vegetation for oviposition (*Juncus*). It is interesting to note that the individuals recorded at pond P1 belong to the sample displaced at a distance of 1000 m, at a site located farther from their marking pond than pond P1, as well as to the sample taken 500 m away, at a site located between their pond and pond P1. Most likely these individuals belonged to the sub-samples released closest to pond P1, but while the individuals displaced to 1000 m could easily meet that pond during their return flight, those displaced to 500 m, in order to reach P1 had to move even farther away from their home pond.

A few dispersed individuals showed a wandering behaviour, that is to say, they did not settle permanently at the pond where they had been first recorded as dispersed. Especially noteworthy are one marked as dispersed at pond T10, and then recorded again at T15, and another one belonging to the sample displaced 1000 m from the pond T1, that was recorded at pond T10 on September 2nd, and again at pond P5 on September 22nd, very close to its home pond (cf. above).

Reproductive behaviour was recorded for dispersed individuals, either marked or unmarked, which indicates the possibility of colonization of non-populated ponds by dispersed individuals.

One of the factors upon which successful colonization of a non-populated pond is based is the number of individuals that manage to reach that pond by dispersal flights. Since, for dispersed individuals, this is a matter of chance, it can be inferred that a pond will be more promptly colonized if it is located near other populated ponds. This can also explain why, after the extinction of the populations of pond T4 (Fig. 1, A) and T1 (Fig. 1, B) in 1977 (cf. above), no individuals could be observed at T1, while some have been at T4 ever since 1978.

Especially noteworthy is the individual of the sample displaced to 1000 m in the reproductive period, which we have mentioned above in relation to homing; this individual at pond T10 mated with a female of the introduced population before moving off to pond P5. In this case it would seem that the homing drive has persisted after the male had found a pond inhabited by a conspecific population (introduced and dispersed insects) where he could successfully mate.

CONCLUSIONS

From the results of these experiments it is possible to draw the following conclusions:

- (1) Astatic pond populations of *L. barbarus* studied are highly philopatric; this adaptation is probably actively selected for by the ponds having a regular water cycle, long enough to allow larval development till emergence. Each individual breeds at the pond at which it spends a number of days immediately after emergence (in natural conditions, its native pond);
- (2) Some non-populated ponds may prove suitable for larval growth and emergence, but they often have irregular water cycles, and this does not allow the establishment of populations surviving through years;
- (3) During the pre-reproductive period (2.5 — 4 months) insects may fly off from their breeding site up to a distance of more than 500 m and perhaps up to 1000 m;
- (4) The return to native ponds for breeding after exodus is based on homing behaviour; it is still a matter of investigation whether dragonflies make some acquaintance with the areas flown over during the maturation period or any orientation mechanism is involved;
- (5) Short-range dispersal actually takes place and is potentially directed towards colonization, but it is such a rare event that colonization of uninhabited ponds is seldom achieved.

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