Odonatologica 17(2): 107-114 *June 1, 1988*

ASPECTS OF DEMOGRAPHY IN *LESTES BARBARUS* (FABR.) AND *L. VIRENS VESTALIS* RAMB. (ZYGOPTERA: LESTIDAE)

C. UTZERI[1], G. CARCHINI[2] and E. FALCHETTI[1]

[1]Dipartimento di Biologia Animale e dell'Uomo, Università di Roma
"La Sapienza", Viale dell'Università 32, I-00185 Roma, Italy
[2]Dipartimento di Biologia, Università di Roma "Tor Vergata",
Via Orazio Raimondo, I-00173 Roma, Italy

Received May 12, 1987 / Revised and Accepted November 6, 1987

Mark-release-recapture data of 3 single-pond populations of *L. barbarus* and 1 of *L. virens* were worked out to estimate: consistence of populations at emergence and at the egg stage, sex ratios at emergence and in the reproductive period, pre-reproduction period duration, survival in the field and dispersal of females in respect to males. On the basis of critical considerations, sex ratio at emergence is suggested to be 1:1, while in the reproductive period it is male-biased. The length of the pre-reproductive period is widely variable in *L. barbarus*, while in *L. virens* it falls within the range of the former. By comparing the length of the pre-reproductive period of *L. virens* populations from central Europe with that of those in central Italy, it is suggested that there is a correlation between latitude and pre-reproductive period length in this sp. as is also known in other lestids. Survival rate in the field was lower in the reproductive than in the pre-reproductive period, probably due to heavier predation in the former. Females dispersed more than males, dispersal rates being widely variable in different samples and years. Evidence of dispersal in teneral rather than in mature damselflies suggests that colonization of new ponds may occur as a consequence of earlier acquaintance with flooded ponds, which can induce the damselflies to home to the new pond after maturation.

INTRODUCTION

The present paper reports on mark-release-recapture data from three single-pond populations of *Lestes barbarus* and one of *L. virens*, mainly collected during preceding research (UTZERI et al., 1976; 1984; 1987) but not discussed formerly. The aim of this paper is to further the knowledge of the biology of these two species, with emphasis on population structure and dispersal.

METHODS

The research was carried out in 1974, 1975 and 1979 in Castel Porziano (Roma) at three temporary ponds which are normally flooded between November and June. These ponds, hereafter named T-1, T-9 and T-21, were about 25, 15 and 40 m in diameter, respectively. Non-quantitative observations were also made between 1980-1986 in the same area. The insects were marked in the emergence period (May-June) and immediately released at their emergence pond. Marking was made on a wing with a car enamel spot, whose colour and position was pond- and date-specific. In the reproductive period (August-October) the marked insects were recaptured on the first day they were spotted at the pond, and were marked the second time, again with a pond-specific but not date-specific mark. However the number of recaptures was recorded on each day.

In 1974, censuses were made of the damselflies which were present at ponds T-1 and T-9 in the reproductive period, by counting and marking each individual once. Census marks were the same as recapture marks for the damselflies which had been marked in the emergence period.

In 1975, during the reproductive period, a sample of 31 mature males of *L. barbarus* were marked and released at the same pond (T-1). This was used to evaluate the daily survival rate in the reproductive period.

RESULTS

The data on marking, recapture and censuses are reported in Table I.

POPULATION ESTIMATES

Assuming that (1) marking did not increase mortality, and (2) the increase of populations due to incoming colonizers was negligible (UTZERI et al., 1984), then from the emergence to the reproductive period, the populations should have decreased according to the rates of samples marked at emergence. Thus, the size (P) of the emerging populations can be estimated by

$$P = \frac{C \times M}{R},$$

where (C) = number of the censused individuals, (M) = number of the individuals marked at emergence and (R) = number of the M individuals recaptured in the reproductive period. By this method, the emerging populations of *L. barbarus* at ponds T-1 and T-9 were 427 ♂ and 414 ♀ (= 841) and 421 ♂ and 376 ♀ (= 797) respectively. As at ponds T-1 and T-9 the females censused were 76 and 43 respectively (Tab. I.), assuming for each a single clutch of 200 eggs (UTZERI et al., 1987), the egg populations could have consisted of at least 15,000 (pond T-1) and 8,600 eggs (T-9).

SEX RATIOS

The sex ratios of the populations of *L. barbarus* censused at ponds T-1 and T-9 in the reproductive period were 62:38 and 67:33, male biased respectively; both differ significantly from unity (chi-squared test; $p < 0.005$ and $p < 0.001$ respectively). At emergence, the sex ratios of the same populations (on the basis of the above estimates) do not differ significantly from unity (chi-squared; $p > 0.5$ and $p > 0.1$ respectively).

The sex ratios of the samples captured randomly for marking at emergence are male-biased: for *L. barbarus*, 54:46 (pond T-1), 66:34 (T-9) and 62:38 (T-21), the latter two significantly different from unity (chi-squared test; $p < 0.005$); for *L. virens*, 54:46 (T-21).

PRE-REPRODUCTIVE PERIOD DURATION

Assuming that (1) each individual was mature when first netted at the pond in the reproductive period and (2) marked individuals had no chance of escaping recapture due to conspicuous markings, the average duration of the pre-reproductive period in the six samples of *L. barbarus* and two of *L. virens* were as reported in Table I, or possible a little longer, as some of the damselflies marked in the emergence period could have been some days old. For all 109 *L. barbarus* males and 40 females from the three ponds, these were 76.3 and 77.5 days. UTZERI et al., (1984) report a 98-days pre-reproductive period for a sample of *L. barbarus*, with no sex sub-samples. This value, however, was obtained by adding some days to individual times elapsed between marking and recapture, to take into account the estimated age of damselflies at the marking dates.

SURVIVAL

Individual daily survival rates in the pre-reproductive period were computed by

$$1 - \frac{M - R}{DM}.$$

where (M) = number of marked individuals, (R) = number of recaptured individuals and (D) = average pre-reproductive period (as number of days) of R individuals. The resulting values for males and females of both species, as well as for the *L. barbarus* sample marked in the reproductive period, are reported in Table I.

Table I

Synopsis of marking-recapture and censusing operations, length of maturation period, survival in the field and dispersal of *L. barbarus* and *L. virens* — [For further informations see the text]

Year	Species	Pond	Marking dates (No. of days)	Samples marked ♂	♀	Sample recapture abs. numb. (%) ♂	♀	Recapture dates (No. of days)	Censuses ♂	♀
1974	*barbarus*	T-1	4-6/6 (3)	126	109	36(28.6)	20(18.3)	13/8-13/9 (13)	122	76
1974	*barbarus*	T-9	21/5-3/6 (6)	67	35	14(20.9)	4(11.4)	14/8-13/9 (13)	88	43
1979	*barbarus*	T-21	1-5/6 (3)	157	97	59(37.6)	16(16.5)	7/8-12/9 (11)	—	—
1979	*virens*	T-21	1-5/6 (3)	142	121	26(18.3)	2(1.6)	7/8-3/10 (15)	—	—
1975	*barbarus*	T-1	18-19/8 (2)	31		18(58.1)		19/8-24/9 (20)	—	—

Year	Species	Pond	Pre-reproductive period days, average ± SE ♂	♀	Daily individual survival ♂	♀	Expected recaptures of males in the pre-reproductive period of females		Difference of recapture %♀ - %♂
1974	*barbarus*	T-1	72.4±1	76.5±1.6	0.9901	0.9893	30.9	24.5%	— 6.2
1974	*barbarus*	T-9	92.1±2	101.7±7	0.9914	0.9913	8.5	12.6%	— 1.25
1979	*barbarus*	T-21	74.9±1.2	72.7±1.8	0.9917	0.9885	61.8	39.4%	—22.9
1979	*virens*	T-21	84.5±3.7	84.0±16	0.9903	0.9883	26.7	18.8%	—17.9
1975	*barbarus*	T-1			0.9647				

DISPERSAL

Recapture rates of females were always less than those of males (Tab. I). As at ponds T-1 and T-9, in the reproductive period, the sex ratios of recaptured samples which had been marked at emergence did not differ significantly from the sex ratios of censused males and females, which had not been marked at emergence (chi-squared test; $p > 0.25$ and $p > 0.50$ respectively), we have no evidence that marking caused lower recapture rates of females.

In *L. barbarus*, the differences in recapture rates between male and female samples of each pond population, relative to loss of males in the same time periods as females (Tab. I), are significant (chi-squared test) for only the population of pond T-21 ($p < 0.005$), but the sum-up of the three chi-squared values still gives a significant value ($p < 0.005$). As we had no evidence of higher mortality for females than for males, we believe that the lower recapture rate of females was probably due to higher dispersal of females.

In *L. virens* too, dispersal was higher in females than in males ($p < 0.005$; Tab. I). Furthermore, *L. virens* females dispersed more than *L. barbarus* females ($p < 0.005$), but the difference between the males of the two species is not significant.

DISCUSSION

POPULATION ESTIMATES

Our estimates of *L. barbarus* populations at emergence are possibly biased by two errors: (1) even if assuming that marking did not directly increase mortality, it might make damselflies more easily detectable by potential predators, thus indirectly causing higher mortality of marked insects. The bronze-green colour of lestids, otherwise, makes them rather cryptic among vegetation. As a consequence, the emerging populations would be overestimated. (2) If any individuals escaped capture within censusing operations, these were more likely to be unmarked (i.e. cryptic) than marked (i.e. easily detectable) insects. As a consequence, the emerging populations would be underestimated. Thus, these errors tend to counterbalance. (3) The number of days the researchers were in the field were almost half the total time span during which recapture and censusing took place (Tab. I), and even if damselflies commonly attend the pond on more than one day of their adult life (e.g. BICK & BICK, 1961), some may have been present at ponds but on days when researchers were not. This however would affect absolute countings but not estimates.

Estimates of the egg populations represent the next rather than the preceding generations of the populations concerned, but given fairly stable populations, these estimates give a rough idea of the decrease of populations between the egg and adult stages. Also egg estimates may be biased by errors: (1) possibly not all of the females oviposit (e.g. BICK & BICK, 1961) and (2) some females can oviposit more than once in their life (BICK & BICK, 1961; LOIBL, 1958; UTZERI et al., 1987). However, these errors tend to counterbalance each other.

SEX RATIO

In several species of dragonflies, UBUKATA (1974) recorded sex ratios not significantly different from unity at emergence. The sex ratios of our *L. barbarus* samples netted for marking at emergence, when significantly different from unity, probably did not represent the real situation, since it is known that among lestids the two sexes can emerge asynchronously (WESENBERG-LUND, 1913; NIELSEN, 1954). But the sex ratios of our populations, as estimated at emergence, are in accord with UBUKATA (1974); this means that the greater number of males rather than females at reproductive sites, which is commonly observed in dragonflies, can be due to males attending the ponds more frequently than females (e.g. BICK & BICK, 1961) as well as to actual structure of the breeding populations.

MATURATION PERIOD

Our data, together with UTZERI et al.'s (1984), show that the length of the maturation period of *L. virens* falls within the range of that of *L. barbarus*, and that, as far as *L. barbarus* is concerned, the maturation period duration can vary in different years or between different populations within the same year (Tab. I).

Nevertheless, this could be related, at least in part, to dates when marking had been performed, with significantly longer duration periods (t-test; $p < 0.005$ for both sexes) for females marked between May 21 - June 3 (90 percent of both samples marked on May 21-24, pond T-9) compared to those of samples which were marked in early June (T-1) (Tab. I). Otherwise, samples marked on corresponding dates of different years (T-1 and T-21) matured in similar time spans (Tab. I). Accordingly, the 98-days pre-reproductive period duration obtained by UTZERI et al. (1984) is relative to samples marked in the end of May.

UEDA (1978) showed that in *L. sponsa*, the length of the maturation period is inversely correlated with latitude, and UTZERI et al. (1984) suggest that the same may occur in *L. barbarus*. In central Italy, *L. virens* emerges in June and breeds from August onwards. Prof. Eberhard Schmidt (pers. comm.) recorded freshly emerged *L. virens*, in Germany, in July and August, and LOIBL (1958) states that in Germany the breeding season of *L. virens* begins in early August. These data suggest that in central Europe the maturation period of *L. virens* is far shorter than in Italy, and that an inverse correlation between length of maturation period and latitude is probably valid also for *L. virens*.

SURVIVAL

The individual daily survival rates of our samples are very similar to those reported by UEDA & IWASAKI (1982) for *L. temporalis* over a period of 61-60 days, which in *L. barbarus* and *L. virens* roughly corresponds to the pre-reproductive period. Lower values for females compared to males probably reflect higher dispersal of the former (cf. below). Daily survival is lower in the reproductive period, which also agrees with *L. temporalis* (UEDA & IWASAKI, 1982). As we had no evidence of any dispersal occurring in the reproductive period (also UTZERI et al., 1984), lower survival rates of males in this period are probably due to higher mortality, perhaps resulting from the crowding at the relatively open habitats of ponds for many hours a day, where damselflies are less protected from predators.

DISPERSAL

MOORE (1954) and BICK & BICK, 1961; 1968) suggest that dragonfly females disperse more than males. UTZERI et al. (1976; 1984) did not distinguish male from female samples of *L. barbarus*, but on the basis of direct observations also suggested a higher dispersal of females. The present data, worked out for equal periods spent in the field by males and females, which attempt to equalize mortality, show that the recovery of females was 1-23% less than that of males in *L. barbarus*, and 17% less in *L. virens* (Tab. I). These differences can be assumed to be due to greater dispersal rates of females relative to males, and show high variability in possibly different situations in *L. barbarus*. Similarly BICK & BICK (1961) recaptured 36% less females than males of *L. disjunctus australis*.

The dispersal of temporary pond populations of *L. barbarus* may be too limited for successful colonization of nearby ponds to take place (UTZERI et al., 1976; 1984). In 1982, several single-pond populations of *L. barbarus* underwent extinction at Castel Porziano due to drought in early spring. Progressive recolonization was then recorded from 1984 onwards, when temporary ponds remained filled until early summer. Colonizers probably came from nearby ponds where damselflies had survived the drought. At the recolonized ponds, no mature adults had been recorded in 1983, but a few tenerals were recorded in late spring 1984, so it seems likely these were dispersed rather than autochthonous. UTZERI et al. (1984) produced evidence for a lack of spontaneous dispersal in the reproductive period; they obtained colonization of a pond previously lacking *L. barbarus*, by putting there a number of teneral specimens before the pond dried out. These damselflies returned to the new pond after maturation. The above observations suggest that colonization can also be carried out spontaneously by teneral damselflies if these, within a few days of emergence, happen to meet a pond still flooded, at which they will stay perhaps to feed on swarming prey. These damselflies will probably return to the new pond after maturation, as in UTZERI et al.'s (1984) experiment. If this is true, dispersal rates and successful colonization could depend on the abundance of still flooded ponds at the time when damselflies depart from their native pond. On the contrary, in relatively dry years, there would be less dispersal, and single-pond populations would tend to remain isolated.

ACKNOWLEDGEMENTS

Programma M.P.I. "Studio della fauna del Mediterraneo Occidentale"; contratto C.N.R. no. 86.00581.04, gruppo "Biologia Naturalistica"; stanziamento M.P.I., quota Facoltà 60%.

REFERENCES

BICK, G.H. & J.C. BICK, 1961. An adult population of Lestes disjunctus australis Walker. *SWest Nat.* 6: 111-137.

BICK, G.H. & J.C. BICK, 1968. Demography of the damselfly, Argia plana Calvert (Odonata: Coenagriidae). *Proc. ent. Soc. Wash.* 70: 197-203.

LOIBL, E., 1958. Zur Ethologie und Biologie der deutschen Lestiden (Odonata). *Z. Tierpsychol.* 15: 54-81.

MOORE, N.W., 1954. On the dispersal of Odonata. *Proc. Bristol Nat. Soc.* 28: 407-417.

NIELSEN, C., 1954. Notule odonatologiche. II. Notizie sul genere Lestes Leach. *Boll. Ist. Ent. Univ. Bologna* 20: 65-79.

UBUKATA, H., 1974. Relative abundance and phenology of adult dragonflies at a distrophic pond in Usubetsu, near Sapporo. *J. Fac. Sci. Hokkaido Univ.* 19: 758-776.

UEDA, T., 1978. Geographic variation in the life cycle of Lestes sponsa. *Tombo* 21: 27-34.

UEDA, T. & M. IWASAKI, 1982. Changes in the survivorship, distribution and movement pattern during the adult life of a damselfly, Lestes temporalis (Zygoptera: Odonata). *Adv. Odonatol.* 1: 281-291.

UTZERI, C., E. FALCHETTI & G. CARCHINI, 1976. Alcuni aspetti etologici della ovipoSizione di Lestes barbarus (Fab.) presso pozze temporanee (Zygoptera: Lestidae). *Odonatologica* 5: 175-179.

UTZERI, C., G. CARCHINI, E. FALCHETTI & C. BELFIORE, 1984. Philopatry, homing and dispersal in Lestes barbarus (Fab.) (Zygoptera: Lestidae). *Odonatologica* 13: 573-584.

UTZERI, C., E. FALCHETTI & R. RAFFI, 1987. Adult behaviour of Lestes barbarus (Fab.) and L. virens (Charp.) (Zygoptera: Lestidae). *Fragm. ent.* 20(1): 1-22.

WESENBERG-LUND, C., 1913. Odonaten-Studien. *Int. Revue ges. Hydrobiol. Hydrogr.* 6: 155-228; 373-422.