SHORT COMMUNICATIONS

POPULATION STRUCTURE
IN *ISCHNURA DENTICOLLIS* (BURMEISTER)
(ZYGOPTERA: COENAGRIONIDAE)

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A mark-recapture study in *I. denticollis* was carried out in a large pond in Mexico, with a high population density. Manly & Parr method was used to measure population size, survivorship and increment rate. There were several daily maxima and minima in population size throughout the study. Minima were attributed to the detrimental effect of strong rains. Survivorship had an average of 0.7053 for both sexes, which converted to days gave 2.86, one of the lowest rates in the Odonata. Maximum longevity was 42 days for males as well as for androchromatic and heterochromatic females. As in other studies males had more constant recapture indices, followed by androchromatic and heterochromatic females. Primary sources of observed mortality were spider predation and falls into the water. The Morisita and variance-to-mean indices suggest an aggregated dispersion pattern for both sexes. Vagility appears to be low. Sex ratios were approximately equal. Maturation time, measured from emergence, was 6-9 days for males and androchromatic females. Comparisons are made with other *Ischnura* spp., but especially with the closely allied *I. gemina*.

INTRODUCTION

Studies using mark-recapture techniques are frequently appropriate for Odonata due to their short lifespans, apparent site-fidelity and, in general, their ease in marking. Population dynamics for various species have been clearly documented by GARRISON & HAFERNIK (1981), CORDERO (1987), HINNEKINT (1987), WATANABE et al., (1988), HINNEKINT & DUMONT (1989), among others.

More studies with other species should provide a comparative basis to help in determining which biotic factors may be unique or are shared with other species. Such studies with congeneric species may also yield demographic and behavioral differences which may give insights into their evolutionary relationships.

Here I present an ecological study of *Ischnura denticollis* (Burm.), a common inhabitant of temperate and subtropical areas of Mexico, which reproduces in lentic waters. I describe and compare several population parameters with data from other species, principally *I. gemina* (Kenn.). These species maintain some behavioral similarities (CORDOBA-AGUILAR, 1992) incurring a degree of hybridization in California (LEONG & HAFERNIK, 1992). I think that the comparison among these two species will be useful for understanding their situations in allopatry and sympatry areas. Besides, *I. denticollis* shares other similar patterns with species of the genus (CORDOBA-AGUILAR & ALARCON-GTZ., 1992), as are the androchromatic/heterochromatic female condition, the androchromatic female with a male-typical behavior, prolonged copulations and a scramble-competition mating system (CORDOBA-AGUILAR & ALARCON--GTZ., 1992).

STUDY AREA AND METHODS

The study was conducted at an artificial, 8 year-old eutrophic pond, located 1 km NE of Xalapa (19°30'N 96°95'W), Veracruz State, Mexico. The pond is about 45 x 16.5 m (Fig. 1) and a maximum water depth of 1.5 m. Other Odonata commonly found there were *Aeshna jalapensis* Wllmsn, *Anax junius* (Dru.), *Pantala flavescens* (Fabr.), *Orthemis ferruginea* (Fabr.), *Telebasis salva* (Hag.), *Acanthagrion quadratum* Sel. and *Archilestes grandis* (Ramb.), all of which are characteristic for disturbed water areas (R.W. Garrison, pers. comm.). In the area only a few *Quercus* sp. trees surround the pond.

The duration of study was from September 8 to November 10, 1991, during which I visited the site every third day (see Tab. II for specific days). I established 478 quadrats of 1 m² covering almost all the pond surface (total surface is 490 m² approx.).

Individuals were numbered on one wing with an indelible ink pen. During the marking procedure I recorded the following set of data:

Fig. 1. Study site. — [Framed: sampled area; — shaded: areas with abundant emergent vegetation].

date, number, sex, activity, estimated age, quadrat and hour. Estimated age was determined using the following criteria: teneral (those individuals almost newly or recently emerged and with non--hardened cuticle); juvenile (cuticle more strongly developed and body colour more conspicuous than in tenerals, and never were seen in copulation); mature (with fully developed coloration and observed in copulation). Age categorization for heterochromatic females was more subjective due
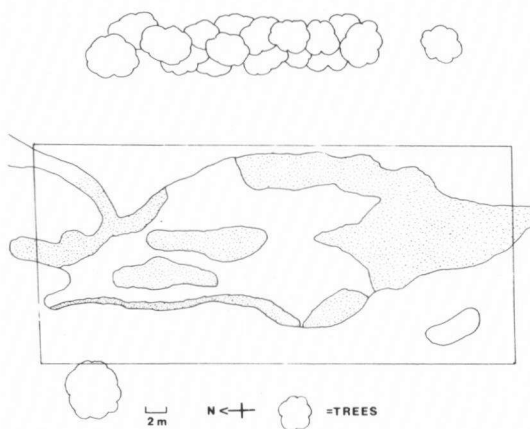
to the difficulty of differentiating between juvenile and mature stages.

Individual recaptures never exceeded two times a day due to the large number of individuals sampled.

Determinations of daily population size, survivorship and number of individuals entering the population (birth rate), were made using the MANLY & PARR (1968) multiple capture and recapture method. Daily survivorship estimates for missing days were obtained using the next equation:

$$\text{Daily survivorship} = (\text{survivorship})^{1/d}$$

where, d represents the number of non-sampled days between two successive samples (SCOTT, 1973). Average survivorship in days was calculated using the method of COOK et al., (1967):

$$\text{Expected life span} = \frac{-1}{\log_e (\text{average survival rate})}$$

Dispersion patterns for both sexes were calculated using MORISITA's index (1959):

$$Iq = \frac{\sum_{i=1}^{q} n_i (n_i-1)}{N (N-1)}$$

where, q = number of quadrats, n_i = the number of individuals captured in quadrat i, and N = the total number of captures adding the other quadrats. In addition, the variance-to-mean ratio (s^2/x, SOUTHWOOD, 1979) was used, computing the variance (s) of individuals and the mean (x). Although variance-to-mean ratios often yield higher values than Morisita's index, in general, both indices are interpreted as follows: < 1 indicate uniform, > 1 aggregated and = 1 random dispersion.

Velocity was independently calculated for each sex, using the method of SCOTT (1973, 1974, 1975): V = D/T, where D is total distance in meters of an individual which in turn is the sum of all daily distances over the entire life span of every individual, and T is the total time in days between first capture and last recapture.

I also describe mortality factors, colour changes in both sexes, and sex ratios of individuals marked at emergence.

RESULTS

A total of 1248 individuals were marked and 626 (40.5%) recaptures made for both sexes (Tab. I). Males exhibited greater recapture rates than females, which is consistent with other studies on coenagrionid damselflies e.g. *Ischnura graellsii* (Ramb.) (CORDERO, 1987), *I. gemina* (GARRISON & HAFERNIK, 1981), several species of *Enallagma* (GARRISON, 1979) and *Telebasis salva* (Hag.) (ROBINSON & FRYE, 1986). Androchromatic females had a higher index than heterochromatic females, presumably because they exhibited greater site fidelity.

Table I

I. denticollis: number of captures (C), recaptures (RC), percent (%RC) and recapture average (RA)

Sex	C	RC	%RC	RA
♀ (androchromatic)	231	77	33.3	0.48
♀ (heterochromatic)	219	59	26.9	0.37
♂	798	490	61.4	1.33
Totals and average	*1248*	*626*	*40.5*	*0.72*

POPULATION SIZE, SURVIVORSHIP AND LONGEVITY

The highest daily population size estimate was on September 26 (around 1400 individuals by the Manly & Parr method), followed by several oscillations on the subsequent days (Fig. 2). Other peaks occurred on September 20 (almost 1000 individuals), October 11 (almost 900) and October 20 (around 720). The smallest population numbers were evidenced during strong rains.

Daily survivorship estimates (Tab. II) yielded an average of 0.7053 or 2.86 days for both sexes.

Table III shows the longevity data. As CORDERO (1989) has pointed out, it is impossible to record this parameter satisfactorily because of the difficulty of obtaining records from capture until last recapture. The data presented here must be interpreted with caution, since the samples are very small and only individuals with the higher number of recaptures from teneral were selected for the maximum longevity estimates.

The similarity of the number of days for both sexes and forms of females is remarkable, and the 42 days is one of the longest periods obtained for a damselfly. Values
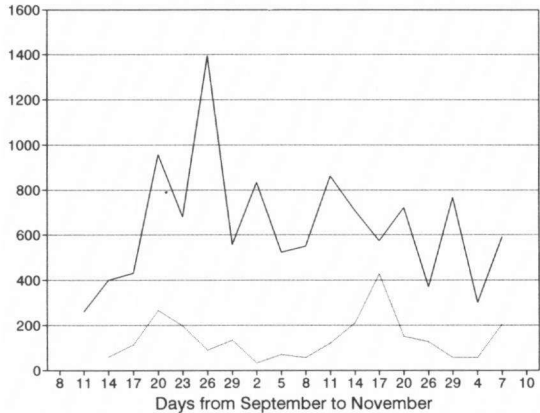

Fig. 2. *I. denticollis*: population size (heavy line) and the increment rate (thin line).

Table II

I. denticollis (both sexes): population parameters, estimated according to MANLY & PARR (1968). — [N_i = total population estimates; — Φ_i = survival rate (in parentheses correction to one day); — β_i = number of new animals joining population]

Date		N_i	Φ_i	β_i
Sept.	8	–	–	–
	11	260.9	0.9004 (0.0974)	–
	14	400.5	0.2281 (0.6911)	59.92
	17	431.05	0.2834 (0.7296)	113.51
	20	956.8	0.6163 (0.886)	265.69
	23	680.9	0.205 (0.6729)	196.21
	26	1396.5	0.1292 (0.5995)	88
	29	558	0.0956 (0.557)	133.61
Oct.	2	832.9	0.0598 (0.4945)	33.37
	5	524.9	0.0836 (0.5378)	69.7
	8	550.9	0.1062 (0.5709)	55.79
	11	863.03	0.2179 (0.6832)	120.05
	14	709.6	0.2441 (0.7029)	210.69
	17	573.8	0.604 (0.8816)	428.66
	20	722.8	0.2597 (0.7138)	149.05
	26	371	0.1741 (0.779)	125.89
	29	767.3	0.1502 (0.6225)	55.73
Nov.	4	299.2	0.0752 (0.6912)	57.1
	7	594	0.6188 (0.9086)	204.03
	10	–	–	–

of other *Ischnura* species are shown in Table IV.

More males lived for nearly as long as the maximum recorded lifespan (42 days) than did either of the two forms of females. For example, five males lived for 36 days, one lived for 39 days, while only one androchromatic female lived for 36 and another eight for 30 days. These discrepancies are partly due to the greater site fidelity exhibited by males, but I can not account for the higher recapture rates for androchromatic females compared to heterochromatic females.

Table III

Maximum longevity (days) in *I. denticollis*

Sex	Max. longevity	n
♂	42	7
♀ (heterochromatic)	42	1
♀ (androchromatic)	42	2

Table IV

Maximum longevity (days) in different *Ischnura* species

Species	Max. longevity	Reference
elegans	50	HINNEKINT (1987)
gemina	36	GARRISON & HAFERNIK (1981)
graellsii	33	CORDERO (1987)
cervula	15	DICKERSON et al., (1992)
posita	9	ROBINSON (1983)

MORTALITY

Although two species of frogs (*Bufo valliceps* Wiegman and *Smillisca boudini* Dumeril & Bibron) were found at the pond, I never observed predation on *I. denticollis*. I found 21 dead marked individuals of which 8 were trapped in spider webs (*Leucauge argyra* (Walckenaer) and *Leucauge* sp., *Theridion* sp. and an undetermined species of Linyphiidae) and 13 were found in the water (Tab. V). The major number of dead individuals in the water, both marked and unmarked, occurred in the days of strong rains.

Table V

I. denticollis: adult casualties recorded during the study

Sex	No.	Location (n)
♂	15	Spider web (6) water (9)
♀ (androchromatic)	2	Spider web (1) water (1)
♀ (heterochromatic)	4	Spider web (1) water (3)

The higher mortality figures in males probably do not reflect the actual male longevity, but are rather due to the circumstance that the males spend more time at the reproduction sites than the females do (see below), therefore their casualties are more easily detected.

DISPERSION AND MOVEMENTS

Calculations of variance-to-mean ratios yielded a value of 4.6 and a value of
2.2 for the Morisita's index in an analysis for both sexes, indicating, nor surpri-
singly, a significantly (p < 0.0001) aggregated distribution of adults. My observa-
tions during the study support these findings since adults were unevenly distribu-
ted about the perimeter of the pond: males aggregated at perch sites along areas
of emergent vegetation where they
intercepted incoming ovipositing fe-
males.

Females on average moved fur-
ther each day than did the males
(Tab. VI). Twenty-six heterochro-
matic females moved a total of 40
m over their lifespan while only a
few (n=5) males exceeded 25 m. Se-
venty percent of males had a ten-
dency to remain in reproductive sites
with few movements as was also
found for androchromatic females.

Table VI

I. denticollis: velocity patterns in males and hetero-
chromatic females, using the SCOTT (1974, 1975)
method

Parameter	♂ (n=80)	♀ (n=47)
Mean T (days)	17.73	17.1
Mean D (m)	12.71	11.09
Mean V (m/day)	1.39	1.54
R maximum	6.5	9.8

SEX RATIO, MATURATION AND COLOR CHANGES

Because marking of fully mature adults yielded operational sex ratios of ap-
proximately 2:1, in favor of males, I attempted to determine true sex ratios by
counting only teneral individuals. Of the 125 marked tenerals, 66 were males
and 59 were females, giving a ratio not significantly different from unity
(x^2=0.288, p < 0.05). Difficulty in identifying the forms of teneral females
prevented me from accurately giving a value for the proportion of each type
emerging.

The maturation time was calculated as the number of days elapsed between
emergence and the appearance of full coloration (or first copulation) in the
respective (marked) individual. It amounted to 6-9 days, both in males (n=12)
and in androchromatic females (n=2), but no data were obtained for heterochroma-
tic females, since these returned to the reproduction sites as late as after more
than 20 days. These values are in the temperate zone congeners as follows: *I.
graellsii* 2-5 days (males) and 4-6 days (females) (CORDERO, 1987) and *I.
gemina* 5-7 days (males) and 7-10 days (heterochromatic females) (GARRISON
& HAFERNIK, 1981).

Table VII documents ontogenetic thoracic colour changes in laboratory kept
I. denticollis, taken from 24 individuals, 8 ♂ and 16 ♀, representing both female
colour forms. Body pattern of heterochromatic females gradually become obscure

Table VII

I. denticollis: age-conditioned colour change

Relative age	♂ and androchromatic ♀	Heterochromatic ♀
Freshly emerged	Dark gray	Light brown
Juvenile-mature	Green-yellow Green-blue	Dark brown
Adult-mature	Blue Darked blue	Opaque blackish

with advancing age, while both males and androchromatic females retain their body patterns, but exhibit a pale body coloration from green to dark blue. Similar colour changes were reported for *I. graellsii* (CORDERO, 1987), though androchromatic and heterochromatic body patterns are different in the two species.

DISCUSSION

Several ecological parameters, indirectly reflect some behavioral sex differences. The parameters affected may include: capture and recapture percent in males and different types of females (the sex ratio was not affected because I was counting only teneral individuals), velocity, and even longevity. The recapture percentage was higher in males than in females, since the former exhibit a greater site fidelity than the latter. Male-like androchromatic females, though more vagile than males, were more frequently seen and recaptured than heterochromatic females. Taking into account that heterochromatic females make only few visits in different places to copulate (with long distances among the sites) and do not remain there, their velocity and range must be greater than in males. The fact that only the heterochromatic females moved further than 40 m, while the males only moved 25 m, draws attention to these differences. The higher recapture figures and the correspondingly longer average lifespans calculated for males as compared with females may also be an artifact of my sampling program: females may live as long as males, but the failure of recapture of marked females may be due to emigration rather than to mortality.

Daily survivorship estimate in *I. denticollis* (2.86 days) is lower than the values given by GARRISON & HAFERNIK (1981) for *I. gemina* (20.3 and 20.2 days) and by PARR & PARR (1979) for *Ceriagrion tenellum* (17.5 days). Survivorship estimated for *I. elegans* in Europe, cited by GARRISON & HAFERNIK (1981), ranges from 3.3 to 13.5 days. In *Enallagma cyathigerum* the average rate is 4.68, while in *Argia vivida* it goes from 3.02 to 9.22 days (GARRISON, 1978), and ROBINSON & FRYE (1986) found in *Telebasis salva* 7.06 days.

The findings on the movements in *I. denticollis* are similar to the data from both heterochromatic females and males of *I. gemina* (GARRISON & HAFERNIK, 1981), showing that the latter species moves more than *I. denticollis*.

In contrast to my study, CORDERO (1991) showed that the two female forms of *I. graellsii* have about the same longevity. This author, using laboratory reared specimens, found similar overall survival rates with field marked individuals. Males of *I. gemina* had greater lifespan estimate than females (GARRISON & HAFERNIK, 1981). It would be of considerable interest to verify these data with long-term studies in *I. denticollis* because my preliminary results are still not clear.

The sex ratio in *I. denticollis* was similar to that of other species. In *Coenagrion puella* it is not significantly different from unity (BANKS & THOMPSON, 1985) and GARRISON & HAFERNIK (1981), sampling larvae from the related *I. gemina*, found a slight but not significant deviation in favor of males. CORDERO (1987) also reported no significant differences in sex ratio for the European *I. graellsii*. The only exception of sex ratio has been cited by Ubukata (1974, *in* UTZERI et al., 1988) with values different from one in some species.

I. denticollis, especially males, were highly aggregated about some specific areas of the pond which had abundant vegetation, where females searched for oviposition sites. In these areas many androchromatic females occurred and, to a lesser degree, heterochromatic females also. Notwithstanding, androchromatic females were always less active in these sites and, in general, were found in small groups from three to eight individuals, with few intra and interspecific interactions (during the study I saw only 10 ovipositions by androchromatic and more than 70 by heterochromatic females). In general, 90% of all matings I saw were carried out by heterochromatic females.

During cloudy days, *I. denticollis* exhibits a similar behavior as reported in *I. graellsii* (CORDERO, 1987), *I. gemina* (GARRISON & HAFERNIK, 1981) and *I. elegans* (Parr, 1973, *in* GARRISON & HAFERNIK, 1981). In days with little rain and calm winds I frequently observed displacement flights and reproductive activities.

The low estimates of daily survivorship in *I. denticollis* could be due to dispersion, marking effect, or mortality from predation in the teneral or juvenile stage. Predation occurs around the pond at open sites without vegetation (see Fig. 1). On the other hand, areas with abundant vegetation, inside the pond, which were occupied by adults, provided protection from predators. However, it seems that predators do not play a strong role on adults.

Predators, particularly spiders and frogs, probably regulate numbers of young *I. denticollis*, but I have little quantitative data supporting this view. On the other hand, CORDERO (1991) describes mortality due to falls into the water, spider webs and predation by aquatic insects for *I. graellsii*, but does not mention predation by frogs or birds. In *I. gemina*, HAFERNIK & GARRISON (1986) did not observe predation by birds or other predators in either sex or, presumably, female forms.

Another interesting question to address is the proportion of androchromatic females in *I. denticollis* and its closest species *I. gemina*. In *I. denticollis* there

exists a higher proportion of androchromatic than heterochromatic females. Some North American populations of *I. gemina*, where it is sympatric with *I. denticollis*, have a minor or non-existent proportion of this female form. I have not counted androchromatic female numbers of *I. denticollis* in those areas, but it is clear that, even for similar sites, ecological pressures are different in temperate and subtropical areas.

In addition, *I. gemina* is confined to a few areas in California (GARRISON & HAFERNIK, 1981) while *I. denticollis* has a wider distribution. Considering their behavioral (CORDOBA-AGUILAR, 1992) and morphological (LEONG & HAFERNIK, 1992) similarities, these different distributions require more study.

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