A MARK-RECAPTURE STUDY OF COEXISTING ZYGOPTERAN
POPULATIONS

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An analysis is presented of the coexistence of 8 spring spp. in an area in Eastern Flanders, Belgium. By counting exuviae and by the mark-recapture method, the behaviour of the different spp. in space and time was followed. The data include estimates of the translocation within the area and estimates of population size and survival rate using the method of Jolly and Seber and a new regression method. — Between spp. (of different genera), differences in spatial and temporal performance were noted which result in a reduction of interaction, whether or not truly competitive. However, between the co-existing sibling spp., *Coenagrion puella* and *C. pulchellum*, no major differences in utilisation of the environment could be found. There are indications that ♀♀ of *C. puella* were driven out of their favored areas, but inspite of this they continued to oviposit at the peak density of *C. pulchellum*. This observation leads to a reconsideration of the competitive exclusion principle.

INTRODUCTION

DUMONT (1971) described the history of the Odonata of the "Wellemeersen", an area in the lower part of Belgium with a variety of artificial waters: bomb-craters transformed into fishing ponds, medium sized ponds (surface area ⩾ 0.25 ha) and a large pool of 20 ha. Between 1957 and 1969 he visited the area regularly and during this period several new species entered the area. If the intrusion was successful, there was often an effect on the species already present. The most striking example concerns the closely related species *Coenagrion puella* and *C. pulchellum*. Up to 1960, when *C. pulchellum* was first seen, *C. puella* was abundant on all types of water. After that time *C. puella* gradually became restricted to the bomb-craters (not populated by *C. pulchellum*), save for a small

population on the ponds, flying late in the season, after the main flight period of
C. pulchellum. This description suggests a competitive exclusion of *C. puella* by
C. pulchellum, except when the former can avoid interactions through a segrega-
tion from the latter in space or time. The two species do not usually occur to-
gether in the Netherlands and Belgium, *C. pulchellum* being a species of more
eutrophic habitats than *C. puella*.

The competitive interactions which are most likely are competition for food
in the larval stage and behavioural interactions in the adult phase, mentioned in
the literature as "mutual interference" or "competition for space". Strictly the
term "competition" should be used only in situations where there is a direct,
negative effect on the population size, either via increased mortality or reduced
fecundity due to starvation, or via disturbance of the reproductive process due
to behavioural interactions (rendezvous of the sexes, copulation and oviposition).
The literature contains much more evidence for mechanisms which probably
reduce the intensity of competition, than examples where competition has been
shown to be actually important in the field. Mechanisms reducing competition
may consist of a specialisation in feeding behaviour or a segregation in space and
time of the potentially competitive populations. These mechanisms may develop
locally in coexistent populations (e.g. "character displacement") or become
characteristic for a species over its whole range. In the early stages, competition
can then be shown to exist and cause a selective pressure.

MACAN (1964) described the coexistence of two zygopteran species, *Enallag-
ma cyathigerum* and *Pyrrhosoma nymphula*, in a situation where there is
evidence that food, or number of feeding sites, in the larval stage is the main
factor limiting population size. The larvae of the two species were segregated
both in microhabitat and in time. Segregation in time of larval growth and emer-
gence of adults has also been shown in coexisting Anisoptera (BENKE & BENKE,
1975) and Lestidae (INGRAM, 1976). Temporal segregation in the larval stage
implies temporal segregation in the adult phase, so it is difficult to distinguish
the phase where the main advantage occurs. As Benke & Benke point out, tem-
poral segregation of larval growth may not be very effective because of a large
overlap in food size and because a competitive interaction might be replaced
by a predator-prey interaction.

In the adult phase competition for food seems less likely than in the larval
stage, as the density of individuals on land is much lower than in water. But it
appears that measurements of daily food intake by adults, compared to the
amounts of food available, have never been made. Behavioural interactions in
the adult phase, related to mating, are spectacular and might be interpreted as
competition for space. MOORE (1964) stated that intraspecific aggression
regulates the density of males at the water, but he did not believe that one
zygopteran species could exclude males of other species from the waterside.
Also, although there are many observations of interspecific aggression of males

at water, we cannot call this competition before it is shown that this aggression leads to a reduced chance of copulation of the females and subsequent success-ful oviposition. Male sexual aggression at the water results in higher chances of reproduction for individual males and hence in a selective pressure in favour of aggression, but does not necessarily increase the chance of reproduction of females, on which the population size depends.

Most studies of interspecific behavioural interactions have concentrated on reproductive isolation and the way in which species-recognition is accomplished. Differences in place and time of mating clearly contribute to interspecific isola-tion. In a study of two sympatric *Enallagma*-species, TENNESSEN (1975) could find such differences, but an ethological barrier involving physical contact often had to prevent interspecific copulation. In such a situation the presence of one species clearly is a hindrance to the other, but success of oviposition needs not be affected. Much adult behaviour seems directed to reducing the hindrance of ovipositing females by males of the same or other species: oviposition directly following copulation, attended by the male; defense of the place where the female is ovipositing (sometimes real territorial behaviour of males); oviposition by the females in the evening when the males have left the water, as in some aeshnids and *Ischnura elegans* (cf. below). Perhaps even "male mimicry" of the oldest females of one of the colour lines of *I. elegans* functions in this way. These adaptations suggest that behavioural interactions are potentially impor-tant, but the ultimate test remains the success of oviposition.

One other aspect has to be mentioned, regarding the "character convergence" thesis reviewed by CODY (1973). Character convergence may consist of devel-oping common signals in territorial behaviour of different, coexisting species, thus leading to the avoidance of time- and energy-consuming interspecific com-petition, by means of interspecific territoriality. Most of the examples Cody mentions are valid for birds, but he thinks the same principle might apply to other groups with interspecific territoriality, such as the Odonata. This inter-specific territoriality may be advantageous in the case of competition for food or oviposition sites (common resources), but for the competition-like beha-vioural interactions in sexual behaviour the time and energy spent in inter-specific interactions are larger the more the species-recognition is restricted to the later stages of the behavioural chain (cf. TENNESSEN, 1975).

According to the description of DUMONT (1971), some form of competition must have existed or still exists between *Coenagrion puella* and *C. pulchellum*. The research reported here was set up to obtain evidence for competition in the field, to study the nature of this competition and to possibly find mechanisms resulting in reduced competition. For this purpose all eight zygopteran species, present in the study area in spring, were studied. A comparison was made be-tween the "Kleine Zavelput", a medium sized pond with a complex pattern of coexistence, and a small bomb-crater with a monospecies-population of *C. puella*.

To obtain some insight in the coexistence of larvae the pattern of emergence was studied by counting exuviae. For analysis of the adult phase the mark-recapture method was used.

STUDY AREA AND WEATHER

A detailed description of the Wellenmeersen was given by DUMONT (1971) and VAN STALLE (1976). The present study concentrated on the "Kleine Zavelput" (pond P1 of Dumont) and a small bomb-crater (not mentioned by Dumont). In Figure 1, the main catching areas are marked: A, B and C are the three sides of the pond (Fig. 2); D (Fig. 3), G and H are former haylands with a coarse-structured vegetation (D is shadowed by a sparse *Populus* plantation); E and F are on a railway talud and adjacent footpath, separating this pond from the "Grote Zavelput" (No 3 in Fig. 1). Between B, D, F and H is a dense woodland and directly behind C is a more open woodland dominated by alder shrubs, bordering G.

Fig. 1. Schematic map of the area. (Letters indicate catching areas; the striped areas are woodland, the white ones have a rough herbaceous vegetation): (1) Kleine Zavelput; – (2) bomb-crater; – (3) Grote Zavelput, seperated by a railway-dike.

The bomb-crater (No 2 in Fig. 1), diameter 5 m, is surrounded by hayland and partly shadowed by trees. Between the bomb-crater and the "Kleine Zavelput" there is woodland and several open areas, partly former haylands.

The field work was commenced on May 18, 1974, which was rather late since the second part of April and the first part of May were exceptionally sunny, resulting in an early emergence of dragonflies. The second part of May and the month of June had an exceptionally high rainfall, but temperature and amount of sunshine were normal (according to the Royal Metereological Institute of Belgium at Ukkel). July started with a lot of rain and sampling was concluded on July 12.

EXUVIAE

METHODS FOR COUNTING

Every other day exuviae were collected at nine sampling sites of 1 m shore-line each, three on each side of the "Kleine Zavelput". The sampling sites carried mainly *Carex* and shrubs of alder. The distinction between exuviae of *C. puella* and *C. pulchellum* was difficult, especially for specimens missing the caudal lamellae.

SPATIAL DISTRIBUTION OF EXUVIAE

The total numbers of exuviae collected at the different sampling sites differ clearly (Tab. 1). Both the structure and the location of the sampling sites seem to be important. The structure of some of the sites (e.g. A3) changed considerably

Fig. 2. View of catching area D_1, looking towards D_2.

during the study: floating plants like *Hydrocharis morsus-ranae* appeared and disappeared with changing wind directions, while other plants emerged and were subsequently removed by gardeners or eaten by rats. These changes in structure were reflected in the number of exuviae found at such site. The location of the site was also important: on the sites near the edges of the pond fewer exuviae were found than in the middle; also larger numbers were found on side B (which faced South) than on sides A and C.

Although, because of these differences, we cannot extrapolate the results from the 9 sites to the total length of shore (ca 120 m), we may compare the relative distribution over the sampling sites of the different species, provided their time of eclosion does not differ too much. The patterns of *C. puella* and *C. pulchellum* do not differ significantly and that of *Ischnura elegans* is in agreement with their combined pattern. There is a significant difference between *Erythromma najas* and *E. viridulum*, but this may be a side effect of their sharp difference in time of eclosion (cf. below) and hence of the changing structure of the

sampling sites. Exuviae of *Cercion lindeni* were mainly found at A2.

In conclusion, there are few indications for spatial patterns in the horizontal distribution of larvae, except for *C. lindeni*. However, this does not exclude a segregation according to depth.

Table I

Distribution of exuviae of the different species over the sampling points (three on each side of the triangular "Kleine Zavelput"

Species	Sex	No. of exuviae at sampling points									Total	% ♂♂
		A1	A2	A3	B1	B2	B3	C1	C2	C3		
Platycnemis pennipes	♂	0	2	1	1	1	1	0	0	1	7	
	♀	0	0	0	1	1	0	0	0	0	2	
	total	0	2	1	2	2	1	0	0	1	9	78
Cercion lindeni	♂	0	6	1	0	1	1	0	0	0	9	
	♀	3	7	1	0	1	1	0	0	0	13	
	total	3	13	2	0	2	2	0	0	0	22	41
Coenagrion puella	♂	5	12	3	17	13	3	2	10	6	71	
	♀	6	4	7	16	11	6	3	8	4	65	
	total	11	16	10	33	24	9	5	18	10	136	52.2
C. pulchellum	♂	6	30	5	45	31	11	11	24	21	184	
	♀	6	17	4	25	24	7	6	20	12	121	
	total	12	47	9	70	55	18	17	44	33	305	60.3
Erythromma najas	♂	3	38	20	24	31	8	9	15	7	155	
	♀	4	39	24	33	37	10	5	19	6	177	
	total	7	77	44	57	68	18	14	34	13	332	46.7
E. viridulum	♂	2	17	1	30	16	7	10	10	12	105	
	♀	5	21	6	23	14	10	14	10	16	119	
	total	7	38	7	53	30	17	24	20	28	224	46.9
Ischnura elegans	♂	11	50	20	79	57	18	17	36	41	329	
	♀	13	45	18	78	59	16	23	22	27	301	
	total	24	95	38	157	116	34	40	58	68	630	52.2
Pyrrhosoma nymphula	♂	0	0	0	2	0	0	0	0	0	2	
	♀	0	0	0	0	0	0	0	0	0	0	
	total	0	0	0	2	0	0	0	0	0	2	100
T o t a l		64	288	111	374	297	99	100	174	153	1660	51.9

TIME OF ECLOSION

At the start of the study considerable numbers of larvae had emerged already. Figure 3 shows the cumulative number of exuviae in time on a relative scale. As indicated by the broken line in Figure 3, the total number of exuviae found per

day was nearly constant throughout the sampling period, while some of the minor fluctuations can be related to temperature and rainfall. This constancy of the total emergence per day suggests some emergence limiting factors to be competed for by the different species. This might be food necessary for the ultimate larval growth, but it could also be a factor earlier in the life cycle. CORBET (1962) reported that competition for space was an important factor in emergence of *Anax imperator*; this was not observed in the present study. The competitive power in the larval phase might be reflected in the amount of synchronisation of the emergence. In the first period the *Coenagrion* species were dominant, together with *E. najas*. Towards the end, *E. viridulum* was found in the

Fig. 3. Time course of eclosion (cumulative) of *Coenagrion pulchellum* (o), *C. puella* (●), *Erythromma najas* (□), *Ischnura elegans* (x), *Platycnemis pennipes* (▲), *Cercion lindeni* (△) and *Erythromma viridulum* (■) on a relative scale. For absolute totals see Table I. The broken line indicates the cumulative eclosion of alle species taken together.

largest numbers, clearly separated in time from *E. najas*. *Ischnura* seems to fill up the gaps between these two periods with an increased emergence. The only difference between the two *Coenagrion* species was in their synchronisation; the median date of emergence being May 20 for both. The variation in time of eclosion was larger in *C. puella*.

Emergence occurred in the early morning hours on sunny days, but could be delayed by rain and low temperature for a day or more. No difference was noted between the species in this respect, nor in the microchoice of emerging sites, which may be important for the predation of emerging individuals by spiders and treesparrows (*Passer montanus*).
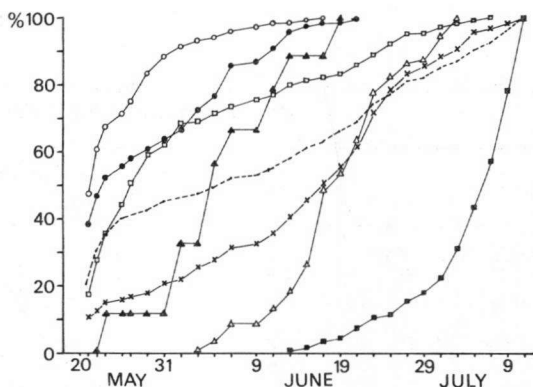
MARK-RECAPTURE STUDY OF THE ADULTS

METHODS

For the mark-recapture study, areas D to H (Fig. 1) were visited twice every day. Areas D, F and G were treated in two seperate parts. During ten minutes

all visible dragonflies were collected; then they were marked, using the indi-
vidual marking technique of HINNEKINT (1974) (Fig. 4) or their recapture
noted, and released at a central
point in the catching area. Several
times during the day, depending
on the weather, sites A and B at
the water were sampled, C only
occasionally. Dragonflies flying
above the water like *Erythromma*
could not be caught in sufficient
numbers. On rainy days the sampl-
ing scheme had to be reduced. The
bomb-crater and surroundings were
sampled in the afternoon, regularly
only after June 11. Irregularly,
catches were made at the "Grote
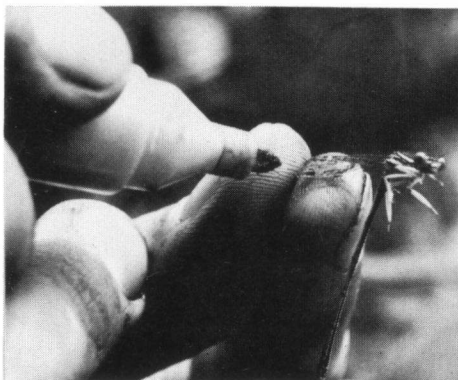Zavelput" to check on exchange
with the "Kleine Zavelput".

Fig. 4. Detail of marking.

ANALYSIS OF DATA

The analysis of the recapture data is based on the following assumptions:
(1) all marked individuals are recognised correctly;
(2) marking has no effect on the probability that the marked individual sur-
    vives, migrates or is recaptured;
(3) all individuals in the population have the same probablity of capture. This
    assumption has a spatial aspect (either individuals mix randomly between
    sampling times or sampling intensity is uniform in space) and a behavioural
    aspect;
(4) emigration is permanent, i.e. there is no immigration of marked individuals.
    With the first assumption no large difficulties have arisen, although with some
colors the marks were difficult to recognise after two weeks.
    The second assumption was tested, using a technique introduced by Robson
(cf. SEBER, 1973). In a contingency table the probability of recapture is com-
pared of individuals first caught and marked to individuals after a subsequent
recapture. This test was applied to the recapure data of *C. pulchellum, C. puella,
I. elegans* and *Platycnemis pennipes* (sexes separate) for the whole sampling
period. No significant differences could be found, indicating that marking had
no greater effect than recapturing on mortality, emigration and probability of
capture.
    With regard to the third assumption, the spatial aspect has been tested in a
contingency table similar to that for the mark effect (Tab. II). There are no

Table II
Distribution of catches of different species among catching areas

			Total no.	A	B	C	D₁	D₂	E	F₁	F₂	G₁	G₂	H	Prob. 1	Prob. 2
Platycnemis pennipes	♂	C	197	9.1 / 0.63	9.1 / 0.53	–	5.6 / 0.82	9.1 / 0.59	5.6 / 0.27	8.1 / 0.35	14.7 / 0.69	15.7 / 0.48	5.6 / 0.42	17.3 / 0.48	0.15	0.17
		R	109 (0.524)	6.6 / 0.10	2.4 / 0.75	–	5.4 / 0.67	10.8 / 0.42	7.8 / 0.25	12.7 / 0.41	11.4 / 0.63	12.7 / 0.58	3.6 / 0.83	26.5 / 0.52	0.17	
	♀	C	166													
		R	93 (0.484)													
Cercion lindeni	♂	C	81	49 / 0.15	2 / 0.5	–	–	1	1 / 1	–	2	1	1	40 / 0.03		
		R	54 (0.11)	10	4	–	–	2	–	10	4	–	4	66 / 0.06		
	♀	C	50													
		R	46 (0.04)													
Coenagrion puella	♂	C	630	15.1 / 0.347	15.1 / 0.431	0.3 / 0.5	14.9 / 0.415	13.5 / 0.412	9.4 / 0.356	6.5 / 0.390	10.8 / 0.427	6.5 / 0.390	6.8 / 0.443	1.1 / 0.286	0.96	0.02
		R	379 (0.398)	14.9 / 0.08	23.0 / 0.27	0.5 / 0.6	16.1 / 0.24	7.5 / 0.25	8.7 / 0.07	5.6 / 0.11	11.8 / 0.05	0.6	8.1	3.1 / 0.40	0.25	
	♀	C	169													
		R	132 (0.172)													
C. pulchellum	♂	C	1439	15.5 / 0.489	14.5 / 0.455	0.1 / 1	22.9 / 0.559	8.3 / 0.538	9.4 / 0.511	9.4 / 0.410	9.9 / 0.406	5.4 / 0.423	3.3 / 0.438	1.3 / 0.421	0.65	0.60
		R	753 (0.485)	14.4 / 0.138	15.9 / 0.139	–	20.8 / 0.309	12.2 / 0.291	8.4 / 0.263	8.2 / 0.243	10.0 / 0.289	5.5 / 0.240	3.3 / 0.2	1.3 / 0.333	0.16	
	♀	C	452													
		R	344 (0.239)													
Erythromma najas	♂	C	75	17 / 0.2	8	2	22 / 0.15	5	18	2	8	8	5	5		
		R	63 (0.18)	7	–	1	0.15	–	0.1	–	0.2	0.2	0.3	–		
	♀	C	61	7	7 / 0.3	4	23 / 0.14	9	13	2	7	15	7	6		
		R	58 (0.05)	–	–	–	–	–	–	–	–	–	–	–		
E. viridulum	♂	C	18	50	6	–	8	–	6	6	11	6	6	11		
		R	18 (–)	–	–	–	–	–	–	–	–	–	–	–		
	♀	C	12	33	–	–	8	–	8	8	16	8	–	16		
		R	12 (–)	–	–	–	–	–	–	–	–	–	–	–		
Ischnura elegans	♂	C	2759	6.6 / 0.313	1.5 / 0.333	–	8.6 / 0.387	14.5 / 0.372	22.8 / 0.317	9.5 / 0.324	9.3 / 0.323	11.9 / 0.324	3.9 / 0.343	11.3 / 0.369	0.61	0.006
		R	1821 (0.340)	8.7 / 0.105	1.8 / 0.115	0.3 / 0.25	9.5 / 0.201	12.3 / 0.207	25.7 / 0.203	8.1 / 0.237	10.4 / 0.211	9.6 / 0.271	3.7 / 0.185	10.1 / 0.238	0.10	
	♀	C	1461													
		R	1161 (0.205)													
Pyrrhosoma nymphula	♂	C	13	38 / 0.75	54 / 0.63	–	8	–	–	–	–	–	–	–		
		R	6 (0.62)	50	50	–	–	–	–	–	–	–	–	–		
	♀	C	2													
		R	2 (–)													
Total		C	7585	10.9 / 0.303	6.9 / 0.364	0.2 / 0.27	12.9 / 0.407	11.9 / 0.358	17.1 / 0.297	8.5 / 0.325	9.9 / 0.332	9.0 / 0.333	4.1 / 0.332	8.6 / 0.315	0.003	
		R	5051 (0.336)													

C – captured; R – recaptured as fraction of captures. Probability (1): probability of the results assuming equal recapture for all areas; (2) probability of results assuming similar distribution of sexes.

apparent differences between the catching areas in the probability of recapture. As the dragonflies certainly do not redistribute randomly between sampling times (cf. below), the sampling intensity appears to have been effectively homogeneous in space. For the behavioural aspect of the third assumption no direct test is available, and yet it is very important for the estimates to be unbiased (GILBERT, 1973). There is evidence, presented below, that the chances of capture for different groups (sexes or species) may differ by a factor 3. For the males of *Ischnura*, four different age-groups can be distinguished on the basis of the colour of the thorax. For these age-groups we may compare the chances of being recaptured. For teneral, green, bluegreen and blue males the fractions recaptured were 0.241, 0.375, 0.360 and 0.283 respectively (significantly different at the 0.1% level). According to the estimates of Table III these differences are mainly due to differences in the probability of capture and not to differences in survival rate. There appears to be an age-dependent difference in conspicuousness in the catching area or a translocation outside the catching areas, but then from all catching areas with the same probability.

Regarding the fourth assumption, there were some observations of dragonflies migrating from the bomb-crater to D, from M to D and from D to K, but

Table III

Estimates of the daily rate of survival by the method of Jolly-Seber and by the regression method, shown in Figure 7. For the Jolly-Seber method the mean is presented for all estimates in which the critical class contained at least 10 individuals (the number of such estimates is given in brackets).

Species (population and phase where relevant)		Sex	Jolly-Seber Survival rate	Regression method Survival rate	Capture rate
Platycnemis pennipes		♂♂		0.68	0.31
		♀♀		0.59	0.34
Coenagrion puella					
Kleine Zavelput		♂♂	0.66 (5)	0.75	0.19
		♀♀	− (0)	0.62	0.12
Bomb-crater		♂♂	0.87 (7)	0.70	0.31
		♀♀	− (0)	−	−
C. pulchellum		♂♂	0.77 (15)	0.82	0.20
		♀♀	− (0)	0.75	0.07
Ischnura elegans	total	♂♂	0.87 (29)	0.78	0.12
	teneral			0.76	0.08
	green			0.78	0.13
	bluegreen			0.78	0.13
	blue			0.73	0.11
		♀♀	1.07 (7)	0.73	0.09

no data on return from such distances are available. As far as I know, the effect of deviations from assumption (4) have never been investigated. The population estimates obtained in such a situation will apply to an unknown larger region than the catching area and will, moreover, suffer from a heterogeneous probability of capture, as described by GILBERT (1973). The long distance translocations observed will be much more significant for gene flow and colonisation of new areas, than for population size at the original location.

In summary, the main problems arise from the third assumption. This means that the estimates given in the following sections may be biased to an unknown extent.

MIGRATIONS BETWEEN THE SAMPLING AREAS

An analysis of the migrations of marked individuals between subsequent catches is presented in Figure 5. From the individuals caught in a given sampling area the place of the next catch is compared with the expected distribution for random mixing individuals. For *Ischnura* males there is sufficient information to separate the data for different times between two catches. We may conclude that, even after nine days, the probability of recapturing an individual at the original site is larger than random. A more detailed discussion of the migrations of the different species is given below.

ESTIMATES OF THE POPULATION SIZE

The data were analysed with the methods of Manly and Parr and those of Jolly and Seber, as described in SEBER (1973). The Manly-Parr method did not give satisfactory results. Apparently the sampling intensity and population size were too small to give reasonably stable results. As far as estimates could be made with this method (males of *Ischnura*) they were slightly lower than the estimates by the Jolly-Seber method. Figure 6 shows the population estimates by the method of Jolly and Seber for *C. pulchellum, C. puella* (for the "Kleine Zavelput" and the bomb-crater) and *Ischnura*. For the other species no reliable estimates could be obtained. The open signs indicate estimates where the critical class in the calculation (m_i) contained fewer than ten individuals. Simulations indicate that in such situations even the order of magnitude of the estimates may be wrong (SEBER, 1973). The estimates at the beginning and end of the sampling period are less reliable than those in the middle part. The daily estimated variance of the estimate has not been shown as it is of limited value (it correlates with the daily estimate itself: for overestimates of the population size the variance is overestimated too and vice versa). In the first week, and towards the end of the sampling period the estimated standard error is as large as the estimate itself and in the middle period the coefficient of variation is still 25%. The estimates
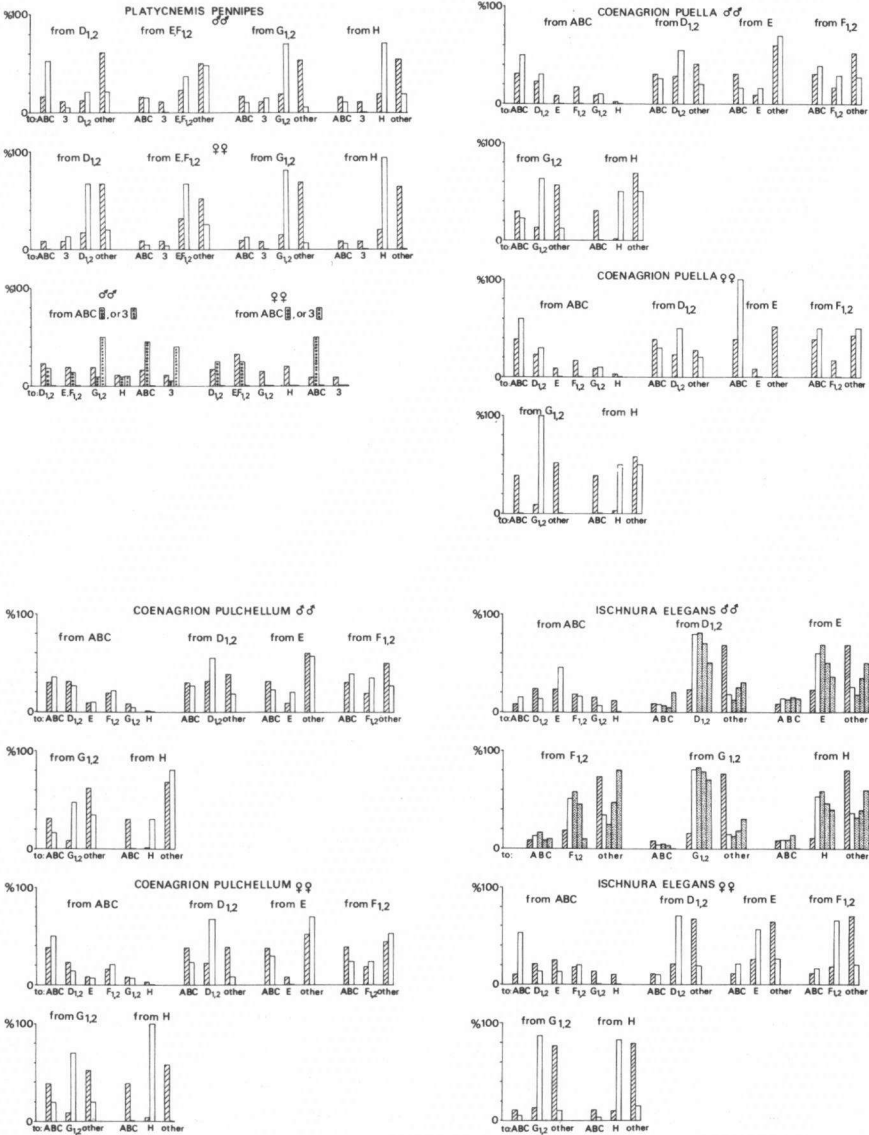
Fig. 5. Analysis of translocation between the sampling areas. The distribution is shown of the site of first recapture after a release in the area indicated. The first column gives the expected distribution on the assumption of random mixing, the second column gives the observed frequency. For *Ischnura* males three other columns are given, representing the frequencies for recaptures after 1 to 3, 4 to 8 and 9 or more days respectively. For *Platycnemis* the "Grote Zavelput" (3) has also been taken into account.
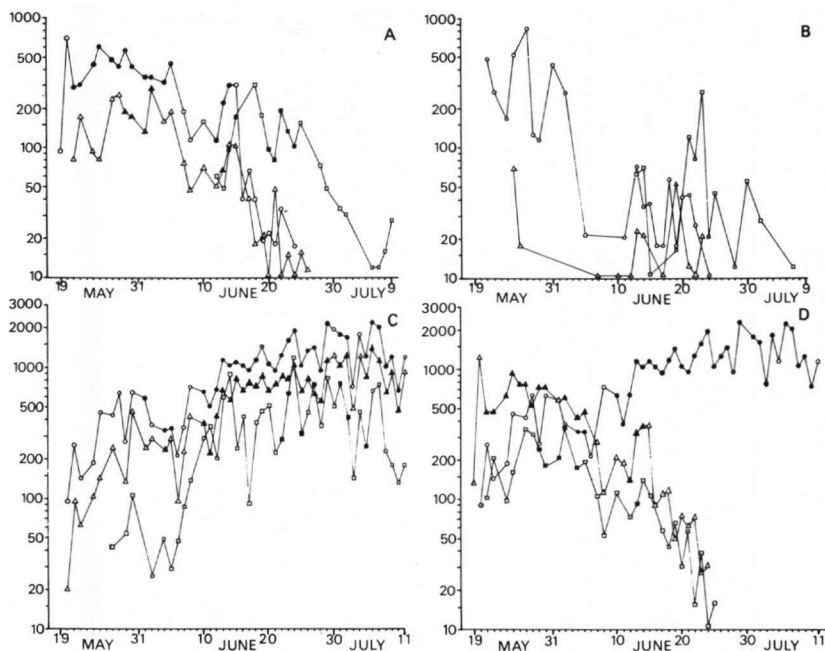
Fig. 6. Estimates of population size by the method of Jolly and Seber. Closed symbols indicate estimates with at least 10 individuals in the critical class, open symbols with less then 10 individuals (this means rather unreliable estimates): (A) Males of *Coenagrion pulchellum* (o and ●) and *C. puella* (△ and ▲) at the "Kleine Zavelput" and *C. puella* at the bomb-crater; — (B) The same as A for females; — (C) *Ischnura elegans* males (△ and ▲), females (□ and ■) and results of combined analysis of male and female recapture date (o and ●); — (D) Estimated numbers of males + females for *Ischnura* (o and ●), *C. pulchellum* (△ and ▲) and *C. puella* (□ and ■) at the "Kleine Zavelput".

for females are the most difficult to obtain, because of a lower sampling intensity. Figures 6 C and 6 D also show the results of an analysis of the combined data for males and females. All these estimates are higher than the estimated number of males plus the estimated number of females. However, the combined estimate is based on a population with heterogeneous sample-intensity and, according to GILBERT (1973), this can result in large errors.

ESTIMATES OF THE DAILY SURVIVAL RATE

The large fluctuations in the population estimate from day to day are to a large extent sampling errors. These errors lead to much uncertainty in the estimate of the daily survival rate, which is derived from subsequent population
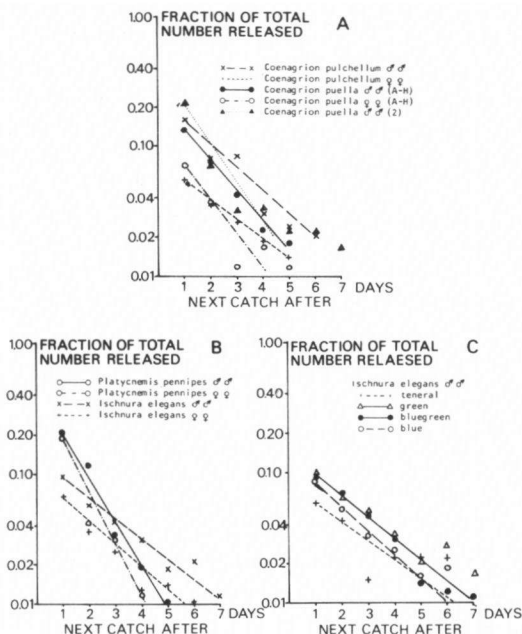
Fig. 7. Regression method for estimating the survival rate, from the times between two subsequent catches. By combination of the fraction recaptured after one day and the slope of the regression line (fitted by eye) an estimate of the mean daily survival rate can be calculated (cf. Appendix).

estimates. The estimate of the daily survival rate frequently reaches values above 1, which are meaningless. It is thus impossible to obtain reasonable daily estimates, but we can still get an estimate of the mean survival rate. This was done with a regression method, based on the time intervals between subsequent catches (described in the Appendix and illustrated in Figure 7). When data for the whole sampling period were combined, reasonable estimates were possible. The linearity of the regression line is an implicit test of the applicability of this model. In most cases a linear regression line fits reasonably well in Figure 7, although deviations occur after three days, when the numbers become small. For the males of *C. puella* near the bomb-crater, there is a tendency to curvilinearity which can be explained by the fact that sampling was not consequently done daily, hence larger intervals are present too often.

The estimates of the regression method are listed in Table III and may be compared with the means of daily Jolly-Seber estimates. (Note that even the mean of 7 daily estimates for *Ischnura* females is above 1). The estimates of the probability of capture lead to population estimates which agree with the

Jolly-Seber estimates but show larger fluctuations from day to day, as might be expected. The differences between the species in the estimated daily survival rate are smaller than the differences in the estimated chance of capture.

The method of Jolly-Seber can also be used to estimate the daily birth rate. However, since this estimate is derived from estimated population numbers and the estimated survival rate, which contain large errors themselves, the estimate of the birth rate is unreliable and frequently leads to negative estimates.

DESCRIPTIONS PER SPECIES

The behaviour of each species in space and time is now considered, using the data presented above and an indication of the position of the males at water (cf. Fig. 8).
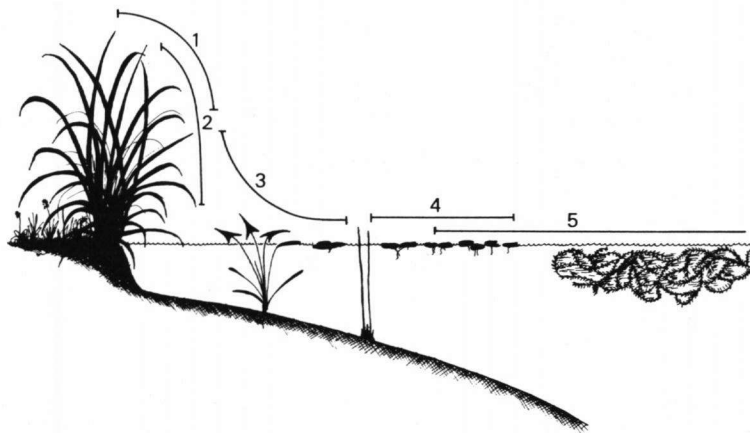
Fig. 8. Schematic transsection through the pond with the main zones of male activity of the different species: (1) *Coenagrion pulchellum* and *C. puella* (high in the *Carex*); — (2) *Pyrrhosoma nymphula* (somewhat lower in the *Carex* vegetation); — (3) *Platycnemis pennipes* and *Ischnura elegans* (in the transition zone with emerging *Sagittaria* and *Butomus*); — (4) *Cercion lindeni* (above the water, close to the shore); — (5) *Erythromma najas* and *E. viridulum*, (above open water).

PLATYCNEMIS PENNIPES (PALL.)

The population size of this species was small, but the sample intensity quite high. In contrast to most coenagrionids, the individuals of this species frequently moved back and forth between the "Kleine Zavelput" and the "Grote Zavelput", and of the individuals caught at the "Grote Zavelput" a similar proportion was recaptured as from the other catching areas. Several times an individual

caught at the water at the "Grote Zavelput" was recaptured the same afternoon in area G. *Platycnemis* was also frequently caught far away from the water (area H). It has a larger flight range than all other species dealt with.

At the water the males are patrolling in the same range as *Ischnura* males, appearing here around noon. In interactions with other species *Platycnemis* males are dominant, on account of their larger size and their enlarged tibiae, which make them very impressive in frontal view. The tibiae of the females show a distinct change in colour during maturation: the tibiae are pink to brownish in teneral females and turn white in mature females. No estimates of the time course of this colour change could be made.

CERCION LINDENI (SELYS)

By the end of June a small population of *C. lindeni* was active on both the "Kleine Zavelput" and the "Grote Zavelput". Possibly exchange between these two ponds is as large as for *Platycnemis*, but insufficient data are available. Most maturing individuals were seen at H, where total zygopteran density was lower than in the other areas. At the water most activity centered around the middle of side A, where most exuviae were found also. According to Dumont (pers. comm.) this has been so since he has been visiting the area. The males fly low above the water, occasionally roaming to the centre of the pond, among *Erythromma*. Tandem formation was seen at the water only.

COENAGRION PUELLA (L.) AND C. PULCHELLUM (VANDER L.)

Near the "Kleine Zavelput" the maximum population size is reached by the end of May (Fig. 6 A, B) after which the population declines rapidly. The trend is the same for *C. puella* and *C. pulchellum*, but the peak number of *C. pulchellum* males is about twice that of *C. puella* males, and by the middle of June the numbers of the two species are equal. In *C. pulchellum* the estimated number of females is slightly lower than the number of males, while in *C. puella* the estimated population size of females in the catching areas is extremely small, suggesting that they stay in other places. In contrast with *C. pulchellum*, there is a statistically significant difference between the sexes of *C. puella* in the areas where they were caught (Tab. II). *C. puella* females are captured relatively more often at the water and in the catching areas far away from the water G2 and H.

For both sexes and both species the chance of recapturing an individual in the area where it was released was much higher than random (Fig. 5 B, C). Direct translocations to the water of individuals from catching areas far away from the water (G and, especially, H) were rare. Individuals caught at the water were also seldom recaptured in area H. This suggests that the individuals far away from the water are mainly in the maturing stage and that sexually mature

individuals are staying in the areas close to the water (e.g. D1). The females of *C. puella* are an exception, staying further away from the water also when mature.

After a visit to the water, both males and females tend to go back to their original area, as may be concluded from an analysis of individuals which were caught away from the water both before and after a catch at the water. For comparison the distribution over the catching areas was used of all individuals recaptured after a catch at the water. For *C. pulchellum* males 8 out of 12 were recaptured in their original area (expected number 4.2), for *C. pulchellum* females 2 out of 3 (1.1), for *C. puella* males 6 out of 10 (3.9) and for *C. puella* females 1 out of 1 (0.25).

The males of both species patrol at the same height above the water, close to the vegetation (Fig. 8), starting in the second half of the morning. *C. puella* males reach their maximum densities at the water earlier in the day than *C. pulchellum* and their peaks are less pronounced. There are no indications for a species recognition between *C. puella* and *C. pulchellum*. It was seen many times that a *C. pulchellum* male tried to mate with a *C. puella* female (or vice versa) but that physical contact prevented tandem formation. The same behaviour of males was seen in catching area D, occasionally resulting in copulation (within one species) away from the water.

For the *C. puella* population at the bomb-crater estimates are available for the second half of June only, but during occasional visits in May hardly any Zygopteran were seen. The *C. puella* population at the bomb-crater clearly reaches its peak densities later in the season, which might be explained partly by the microclimate: the bomb-crater is shaded and the "Kleine Zavelput" is sunny. No climatological measurements were made to confirm this. At the bomb-crater *C. puella* was the only species, except for some *Ischnura*. Exchange with the "Kleine Zavelput" did occur, but did not significantly affect population size. The estimated population size of *C. puella* at the bomb-crater is about equal to that at the "Kleine Zavelput", which means that densities per circumference, area or volume of water (the appropriate measure for mating, oviposition and larval growth respectively [?]), are much higher at the bomb-crater. The population at the bomb-crater was always close to the water: at distances larger than 15 m from the water hardly any individual could be found. The population thus differs both in density and spatial pattern from the population at the "Kleine Zavelput". Both these factors may be interpreted as an indication of competition at the "Kleine Zavelput"; the first indicating the effect of competition (depression of population density), the second the way in which the full strength of competition is avoided.

A critical point for showing competition is a comparison of survival rates in coexisting and single-species populations. A comparison of the survival of *C. puella* at the bomb-crater and at the Zavelput is not clear in this respect, as the

conclusion for the males depends on the estimation method used, and for the females no estimate could be made at the bomb-hole (Tab. III). A comparison of *C. puella* in the first half of the season with many *C. pulchellum* present and in the second half of the season with only a small *C. pulchellum* population is possible only on the basis of Jolly-Seber estimates, which are not accurate at the low sampling intensities. However, it is suggestive that the mean daily estimate of the survival rate is higher in the second period for *C. puella* females, and lower for *C. puella* males and both sexes of *C. pulchellum*. Nevertheless, despite all these indications of competitive interactions, even at the peak of activity of *C. pulchellum*, females of *C. puella* could be seen to oviposit successfully, although this has not been quantified.

ERYTHROMMA NAJAS (HANS.) AND *E. VIRIDULUM* (CHARP.)

Compared to the number of exuviae found, the number of captures of both *Erythromma* species was extremely small. At the water their activity was near the centre of the pond, which made capture impossible. Also in the maturation stage, hardly any *Erythromma* could be found. According to Dumont (pers. comm.) they spend this stage in the alder-brooks. I have not seen this, but the alder shrubs are so dense that they might easily be hiding there. This means that *Erythromma* is spatially separated from the other species both in the maturation and in the mature stage. There seems to be a sharp separation in time between *E. najas* and *E. viridulum* around the middle of June. The flight season of *E. najas* seems to have shortened since the arrival of *E, viridulum* in the study area (it used to last till the middle of July). However, the densities of *E. najas* are certainly not lower than stated by DUMONT (1971). No further information is available about this suggestive interaction.

ISCHNURA ELEGANS (VANDER L.)

The densities of *Ischnura* reach their peak by the second half of June, after the main flight period of *Coenagrion* (Fig. 6 C, D). A large proportion of the captures was in area E, close to but not at the water; but also in areas H and D 2, away from the water, many *Ischnura* were found. The general picture of migrations is the same as in *Coenagrion*: after a catch in any of the areas D to H, a next catch was either at the water or had a high probability of being in the original area; after a catch at the water the next catch was distributed proportionally, except for too few catches in G and H. The effect is even more pronounced than shown in Figure 5: individuals caught in D1 were recaptured more in D1 than in D2 and vice versa, although released at the same point. For the *Ischnura* males the migrations could also be analysed according to the time between two catches. It appears from Figure 5 A that even after a nine-day inter-

val the redistribution is not random.

The males of *Ischnura* are patrolling somewhat lower than *Coenagrion* males, i.e. close to the emergent vegetation (Fig. 8). In *Ischnura* a phenomenon occurred that was rare in the other species: mating is not restricted to the water. Successful tandem formation and copulation were seen in areas E, F and D. In *Ischnura* this is especially effective as oviposition does not usually follow copulation immediately: the females come to the water for oviposition unattended by the males and late in the afternoon when all other zygopterans are gone. This behaviour will ease the colonisation of new areas by *Ischnura* and reduces behavioural interactions with other species.
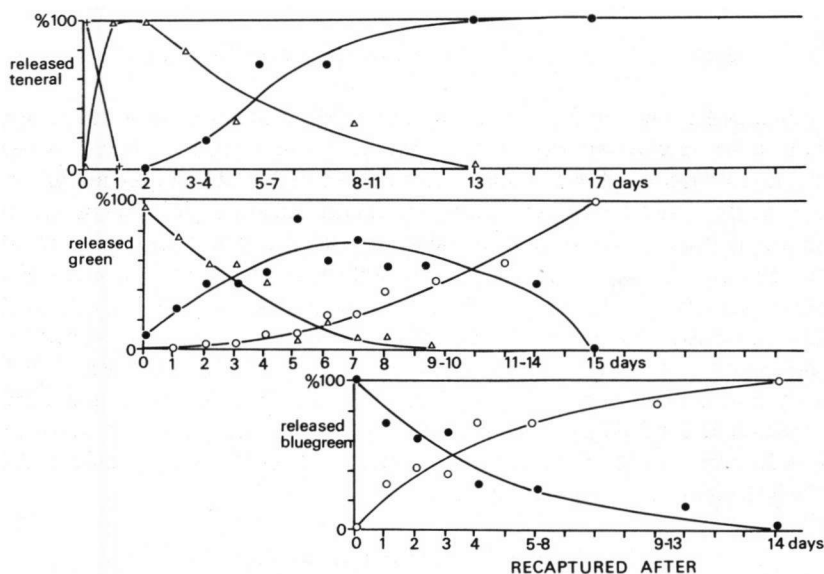
Fig. 9. Pattern of colour change of males of *Ischnura elegans*. The colour of individuals recaptured after a different number of days is indicated for all releases with a certain colour: + = teneral, Δ = groen, ● = bluegreen and o = blue. When combined the same pattern as found by PARR (1973) emerges.

The colour change of the males has been analysed in Figure 9. The result is in agreement with the time course PARR (1973) estimated for a population in Northern England. The recording of the colour in females was not accurate enough to allow analysis of their change. According to Table III the daily survival rate was about the same for all colours of males.

PYRRHOSOMA NYMPHULA (SULZ.)

This species is restricted to the earliest part of the season. After May 18 only a few, old males and females were seen at the water, copulating and ovipositing before the main flight activity of *Coenagrion* in the morning. The flight range of the males at the water is the same as that of *Coenagrion* (Fig. 8).

DISCUSSION

For species belonging to different genera, several differences in behaviour in time and space have been found. The *Coenagrion* species have their own preferred place for staying in the mature phase (i.e. area D) and at the water; *Ischnura* is avoiding interactions by mating away from the water and ovipositing in the evening; the *Erythromma* species differ from other species spatially both in maturation and in the mature phase at the water, and *E. najas* is temporally segregated from *E. viridulum; Cercion* has pronounced spatial preference which is not understood entirely, but may result in less interaction in the maturation phase (in area H). The occurrence of *Pyrrhosoma* only at the start of the season is in clear contrast with the behaviour of this species in more oligotrophic environments, where it may be the only species occurring and can be seen on wings till the end of July. This phenomenon may be interpreted as an effect of competition. Whether its early occurrence in this area is an adaptation to the multispecies situation for avoiding competition, or a direct effect of competition, has to be answered by research on larval physiology and genetic variation. Further temporal segregations are found in the *Lestes* species, which appeared at the end of the study.

In discussing the coexistence of these species attention has to be given to a spring species which is absent at this pond but present in the area, *Enallagma cyathigerum.* *Enallagma* was first seen in the area by DUMONT (1971) at the "Kleine Zavelput", and now occurs exclusively at the large "Gates-pool", where a large population is coexisting with most of the species of the "Kleine Zavelput". The activity of *Enallagma* at the water is in the same range as that of *Erythromma*. However, *Erythromma* is restricted to the occurrence of floating water plants, which are abundant at the "Kleine Zavelput" but scarce at the "Gates-pool", while *Enallagma* also flies above open water. The above spatial differences support the conclusion that a spatial variation in microhabitats, such as is present at the Wellemeersen, is essential to the continued coexistence (or apparent coexistence) of a diverse fauna; a conclusion with direct relevance for the conservation of nature.

Between *Coenagrion puella* and *C. pulchellum* no large scale differences in time and space could be found. There are indications that *C. puella* females are driven out of the areas close to the water in the coexistence situations, as

opposed to their preference in the monospecies situation. However, this does not exclude successful oviposition throughout the season. In the five years since DUMONT's (1971) description, *C. puella* seems to have adapted to the new situation. Of course we need many more data on the way the population densities are regulated, on the limiting factors and on the between-years variations in density, to really evaluate this apparent contradiction of the competitive exclusion principle, stating "complete competitors cannot coexist" (HARDIN, 1960).

BENKE & BENKE (1975), in their analysis of a complex coexistence of anisopteran dragonfly populations, found temporal differences between the main genera co-occurring in their study area, but like this study found that congeneric species had almost identical life histories. Their explanation of this phenomenon is that ecological homologues can coexist because of "errors of exploitation" of the dominant species in an unpredictable environment, but it is not quite clear what these errors are.

Essential in the argument about competitive exclusion is that some species will be more efficient in using the niche than others. Because the probability of exactly identical efficiencies is infinitely small and because differences, however small, will in the long run lead to an exclusion, when the total density is not increasing, the impossibility of coexistence of complete competitors follows. But the smaller the differences are, the longer it will take before the exclusion is accomplished and the time needed for that may be much longer than the time of our observations. More important, this time may be longer than the time required for new adaptations te develop, favouring general fitness instead of favoring specialisation, as in the case of character displacement (niche differentiation). In a fluctuating environment, where the direction of selective forces is continuously changing, there will be more chances for this type of "continued transient coexistence". I would call this explanation not one of "errors of exploitation", but rather one of "continuous co-evolution".

It would be interesting to repeat this study after some years to see whether or not the situation becomes stabilized. The importance of long term observations in the same area is apparent.

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A p p e n d i x

A NEW METHOD FOR ANALYSING RECAPTURE DATA

The method of analysis of recapture data adopted in this paper (Fig. 7) is related to the method used by BEZEM, SLUITER & VAN HEERDT (1957, *Arch. neerl. Zool.* 13: 511-539), but another way of grouping data is used, which has been shown to be more efficient in general (LESLIE & CHITTY, 1951, *Biometrika* 38: 269-292). The analysis depends on two major assumptions, but gives an implicit test of their validity.

Assume a constant daily survival rate q and a constant probability of capture p, in a sampling scheme with regular intervals. When N marked individuals are released initially at t_i, a number $n_1 = p\,q\,N$ are expected to be recaptured at t_{i+1}. Taking into account only the individuals first recaptured, then, at t_{i+1}, $n_2 = (1-p)\,p\,q^2\,N$ (i.e. not caught on t_{i+1}, but caught on t_{i+2} and survived twice) are expected to be recaptured. Similarly, for $n_x = (1-p)^{x-1}\,p\,q^x\,N$ individuals there should be x days between two subsequent catches ($x \geqslant 1$). If we plot $\log(n_x/N)$ against x (as in Fig. 7), n_1 gives an estimate of pq and the slope of the regression line gives an estimate of $(1-p)\,q$. Adding these values we have an estimate of the survival rate q. Deviations from linearity indicate that the model can not be applied.

The use of this method is restricted to situations where a rather long series of samplings at regular intervals is available, with p and q both being approximately constant (at least without a trend in time). It is a convenient method, as data for several releases may be lumped (till say 5 intervals before the last sampling). An individual which is recaptured more than once may thus contribute several recapture-intervals to the total frequency table.