

Colonisation and dispersal patterns of banded (*Calopteryx splendens*) and beautiful demoiselles (*C. virgo*) (Odonata: Calopterygidae) in south-east German streams

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Odonata, Calopterygidae, damsel-flies, colonisation, dispersal, habitat quality, metapopulation, migration behaviour, population density

Abstract. Dispersal behaviour, colonisation and population structure of damsel-fly species were studied in south-east Germany using mark and recapture techniques. The occurrence of damsel-flies at stream sites was correlated with habitat quality, particularly with the stream flow characteristics, riparian vegetation structure and degree of isolation. The damsel-flies had an area specific average dispersal radius of 0.14 to 0.80 km. The maximum dispersal distance observed was 4 km over a 24 h period. Dispersal movements of more than 1 km ranged from 1 to 5% of the population. Dispersal distances depended on habitat quality factors and population density. Movements were not exclusively directed along streams and their tributaries. There was no significant difference in the dispersal behaviour of male and female damsel-flies, although males were recaptured more frequently. To quantify colonisation ability, the study tries to infer the approximate spatial extent of a damsel-fly metapopulation.

INTRODUCTION

Many populations of species occur in discrete patches, which are in spatially isolated habitats. In many patchily distributed populations, local extinction can occur as a result of demographic and environmental processes. Within- and between-population factors (Gill, 1978; Pokki, 1981), such as dispersal between distant habitats, are therefore of great evolutionary and ecological importance (Diamond, 1975; Sukopp, 1984; Mader, 1985). In the so called rescue effect (Brown & Kodric-Brown, 1977; Hanski, 1989), local extinction demands the process of recolonisation as a crucially important event for successful survival (Singer & Ehrlich, 1979). Gene flow between established populations promoted by migration and dispersal is essential in the population biology of some species (Harrison, 1989; Seitz, 1991).

A number of features characterise a good colonist: (1) a propensity to leave the natal habitat; (2) the ability to move long distances over intervening non-habitat; (3) the ability to locate new habitats and (4) the capacity to establish populations from small numbers of founders, once new habitats have been reached (after Harrison, 1989). Previous studies have suggested that *Calopteryx splendens* (Harris, 1782) and *Calopteryx virgo* (Linnaeus, 1758) are fairly sedentary species (Zahner, 1959, 1960; Pajunen, 1966; Klötzli, 1971; Heymer, 1973), characterised by a low tendency for long-distance migration. Their patchy distribution along running waters combined with limited dispersal abilities could result in a tendency towards local extinction and limit the potential rates of colonisation of empty habitats. Despite this, banded or beautiful demoiselles have been observed several kilometres from the nearest breeding sites (Kiauta, 1963; Schmidt, 1986; Wildermuth, 1986; Ott

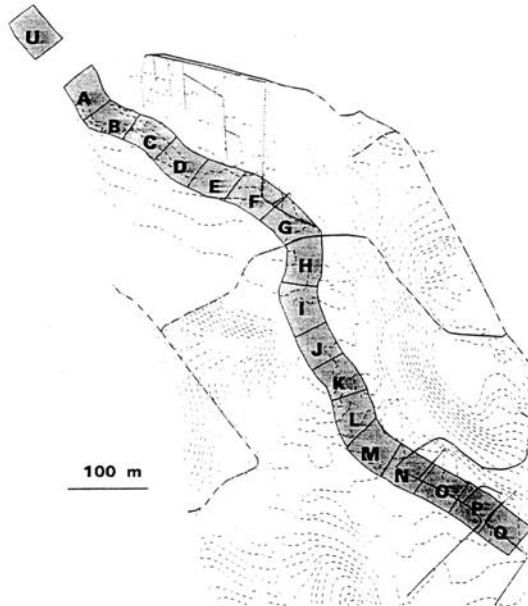


Fig. 1. Map showing main study area Straß divided into 18 patches along the Schinderbach.

(50 m × 40 m), covered approximately 4 ha. Each patch was assigned a specific letter and its vegetation type was described (Fig. 1). Two rheobiotic damselfly species, *C. splendens* and *C. virgo* were used in the investigation. These large and conspicuous damselflies are well suited for such studies, because they are easy to capture and mark. After release they resume their normal behaviour rapidly. Populations of several thousand adults of both demoiselle species inhabit the Schinderbach.

Eight further study areas were selected to cover the full spectrum of streams and habitat patches within a 7 km radius of Schinderbach valley (Fig. 2). All of the streams and ditches in these areas, except two, were inhabited by populations of *C. splendens* and *C. virgo* (Table 1). The distances between the study areas varied between 0.5 and 14 km. Damselflies were captured with hand nets and at their resting sites by hand. Individuals were marked with a sequential number on the fore- or hind wing with a waterproof pen. The patch code letter for the area of capture was also marked on the wings. After marking, the damselflies were released at the site of capture. Using this method, about 50 individuals were marked per

TABLE 1. Site names and Odonata lists for the nine study sites (Cs – *Calopteryx splendens*, Cv – *Calopteryx virgo*, Gv – *Gomphus vulgatissimus*, Of – *Onychogomphus forcipatus*, Cb – *Cordulegaster boltoni*).

Number	Name	Species present
1	Straß	Cs, Cv, Gv, Of, Cb
2	Steinbacherl	Cs
3	Pfaffing	Cs, Cv, Gv, Of, Cb
4	Roßgraben	Cv, Cb
5	Eisgraben	Cv
6	Himmelreich	Cs, Cv, Gv, Of
7	Holzhausen	Cb
8	Kuhbacherl	Cb
9	Ramsauer Bach	Cv, Cb

1987; Didion & Handke, 1989). This suggests that *C. splendens* and *C. virgo* may be able to disperse over relatively long distances to find new habitats and to colonise them successfully. This paper examines whether individuals of the banded and beautiful demoiselle are able to reach and colonise distant habitats, and the prerequisites for the successful establishment of new populations.

MATERIAL AND METHODS

Area of investigation

Experiments were conducted from May to September in 1991 and 1992. The main study area was in the Schinderbach valley, 2 km north-west of Laufen, in south-east Bavaria. The valley supports a range of vegetation types including litter meadows, shrubs, reed stocks and alder forests. The stream itself is unregulated and has a typical meandering structure. The study area, divided into 18 patches of about 2,000 m²

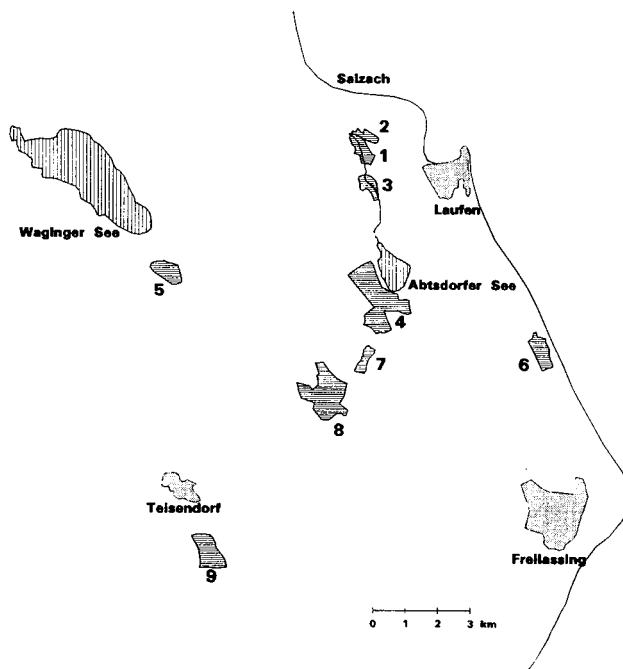


Fig. 2. Map showing location of the nine study sites.

hour. At each investigation patch, mark and recapture experiments were performed for a period of 10–14 days. To reduce handling trauma, marked damsel-flies were kept cool ($< 20^{\circ}\text{C}$) and in darkness for about 30 min. No escape reactions or other alterations in behaviour were observed after release.

Between-habitat movements were studied by releasing damsel-flies away from their original site of capture. Unpopulated or sparsely populated streams considered to be potentially suitable for *C. splendens* or *C. virgo* were chosen as target patches for release experiments. The habitat quality of the release sites was compared with the Schinderbach valley by recording stream structure, vegetation stands and other site quality factors, which may have been important for adults.

In these experiments damsel-

flies were marked and held overnight and released the following morning. About 30 demoiselles were released in the centre of the target patch and another 30 each released from various release points between 0.05 and 2 km away from the target patch. The terrain between the release and target patch consisted of flat meadows or pastures without any topographical or artificial barriers. Damsel-flies were recaptured at the target patch for 10 consecutive days after the release day. The recapture rate for damsel-flies released in the target patch indicated the general turnover rate and ability of capture of damsel-flies. Therefore it was used to calibrate the recapture frequencies of individuals released away from the target patch. Sex- and age-dependent differences in recapture rate were also calculated. To test the possibility of a sex-specific bias in dispersal distances, the ratio of males to females at the release sites and for all recaptures was recorded. The success and continuity of habitat colonisation was estimated as a steadiness rate. Steadiness is the percentage of marked damsel-flies that were recaptured over several subsequent days (between 7 and 10 days) in the same patch.

Data analysis

The mark-and-recapture data were analysed using the method of Jolly (1965). Daily survival and mortality rates were characterised as the turnover rate following the population-dynamic factor of the Jolly method (1965). The turnover rate represents the percentage of individuals in a population that disappear from day_n to day_{n+1} . Significant differences between groups were tested by the means of χ^2 -test or Mann-Whitney U-test (Zöfel, 1988). To test the influence of various biotic and abiotic variables on the population densities of the two damsel-fly species, a correlation matrix, using the data from nine investigation sites (Fig. 2) over one or two years, was calculated (Table 2), using the statistical software MICROSTAT. As a control, two sites (7, 8) were investigated, where no populations of damsel-flies could be found (Table 1).

Various habitat quality variables were calculated for use in the correlation matrix. Vegetation characteristics of each area were recorded following the method of Braun & Blanquet (1964). Ellenberg indices (Ellenberg, 1974) for light and nitrogen were calculated using the PC software VEGAT. Stream quality

TABLE 2. Correlation coefficients and their significance of population density and habitat-quality variables of the 9 different investigation sites studied in 1991 and 1992.

Quality factors	Population density	Significance
Stream width	0.838	**
Degree of shading	0.795	*
Average vegetation height	0.646	ns
Average vegetation density	0.055	ns
Stream quality	0.935	***
Quality of contact areas	0.892	**
Isolation index	0.878	**
Habitat shape index	0.658	ns
Nitrogen index	-0.331	ns
Light index	-0.229	ns

ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

TABLE 3. Classification of the quality for contact areas along the studied stream sites.

Area quality	Classification
1	natural areas without anthropogenic influences
2	mainly natural areas without agricultural influences
3	extensively used agricultural greenland
4	intensively used agricultural greenland
5	arable land (e.g. corn, maize)
6	built-up areas (e.g., buildings, streets)

(SQ) was estimated with an index from 1 to 4 for the natural state of the brook. The saprobic classification (S) was calculated according to Schaeffer & Tischler (1983).

Contact quality (CQ) was estimated using the formula

$$CQ = \frac{A1 + A2 + A3 + A4}{4}$$

where A1–4 are the qualities of the contact areas at each side of the study area. The quality index A is incremental, ranging from 1, for suitable areas such as natural landscapes, to 6 for unfavourable areas, e.g., arable land or streets. The classification of A as shown in Table 3 refers to empirical data of observations during the studies.

The likelihood of a patch being inhabited is influenced by its distance from neighboring populations. The degree of isolation was estimated according to Power (1972). This isolation index (I) is defined as

$$I = 1 - \sum_{i=1}^K 1/m$$

with K the number of populations in a range of 20 km and m the distance of each population with respect to the investigated population.

Since habitats differ in their shape, which may influence colonisation, a habitat shape index was calculated (Faeth & Kane, 1978) according to the formula

$$F = U/2\sqrt{A\pi}$$

with U representing the circumference and A the square dimension of the area inhabited by the population.

RESULTS

Population size estimates for the damsel-flies ranged between 5 and 400 damsel-flies per observation patch. Distribution was heterogenous, with neighbouring patches along the

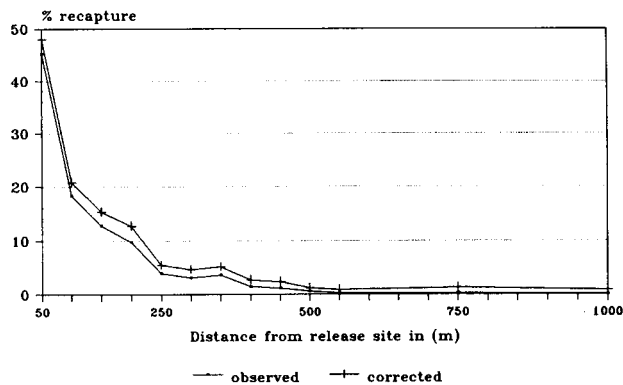


Fig. 3. Migration (observed and corrected) in respect to distance of *Calopteryx splendens* in investigation site Straß (No. 1) in 1991.

population density. Different vegetation associations in the study areas also had an obvious influence on the population density of the damselflies (Table 4). Three investigation patches (F, G, R) had nearly identical values for indices such as stream quality, saprobic index, quality of contact areas, isolation index, shape index and width of the brook, which are highly correlated with population density. Patch T represented a typical example for an agricultural intensively used area. Using the U-Test, the population densities in all four investigation patches were highly significantly different ($p < 0.001$).

Most recaptured adults of *C. splendens* and *C. virgo* dispersed only over very short distances, with about half being captured within a radius of 50 m around the release point. Recapture rates showed an exponential decrease with increasing distance. Dispersal movements of more than 1,000 m were very rare. An analysis of distance-related dispersal of *C. splendens* between subsequent recaptures is presented in Fig. 3. As the population of *C.*

same stream having widely differing population densities. Various quality indices influenced the demoiselle population densities (Table 2). The highest correlation (> 0.9 , $p < 0.001$) was found between population density and stream quality. Vegetation density and the Ellenberg indices for light and nitrogen were apparently not correlated (< 0.3 , not significant) with popu-

TABLE 4. Population estimates for *Calopteryx splendens* and habitat quality characteristics in four investigation patches (F, G, R, T; size of each: 2,000 m²). The investigation patches are situated in the neighbouring investigation sites Nos 1, 2 and 3. Population estimates are the arithmetic mean of data calculated with the Jolly index for 1991 and 1992.

	F (Site 1)	G (Site 1)	R (Site 3)	T (Site 2)
Population density	372	239	109	42
Character	shrub	reed	bank-edge	intensive hay meadow
Vegetational association*	<i>Filipendulo Geranietum palustris</i>	<i>Phalaridetum arundinaceae</i>	<i>Phalaridetum arundinaceae</i>	<i>Arrhenateretum</i>
Covering	100%	100%	95%	100%
Height	10–150 cm	30–200 cm	30–150 cm	10–60 cm
Shading	25–30%	30–35%	25–30%	5–10%
Width	4 m	4 m	4 m	1 m
Isolation	0	0	0	0
Shape index	1.13	1.13	2.64	1.13
Nitrogen	5.3	6.4	6.4	6.0
Saprobic index	2	2	2	2
Stream quality	1.7	1.7	1.7	3

* After Braun & Blanquet (1964)

TABLE 5. Numbers of individuals of *Calopteryx splendens* marked (N) and recaptured (RC) and percent recaptured (% RC) in the observation patches (size of each: 2,000 m²) of study area No. 1 in 1991.

Investigation patch	N	RC	% Rc
A	370	78	21.0
B	95	10	10.5
C	135	22	16.3
D	219	44	20.1
E	229	28	12.2
F	241	60	24.8
G	395	101	25.6
H	70	9	12.9
I	25	3	12.0
J	54	3	5.5
K	32	3	9.4
L	42	2	4.8
M	91	7	7.7
N	483	194	40.2
O	102	32	31.4
P	108	85	78.7
Q	60	12	20.0
U	57	4	7.0
Total	2,808	697	Mean: 24.8 ± 17.5

splendens and *C. virgo* in study area 1 was limited to the extent of the 18 investigation patches (Fig. 1), it was possible to observe the whole range of dispersal tendencies in study area 1. Nonetheless, the calculation of the dispersal distances had to be corrected with the theoretical probability of recapture (Fig. 3). In general there were 18 (the number of plots in Fig. 1) × 2 (the number of possible directions) = 36 possible displacements from the sampling plot. If, for example, a marked specimen moved 50 m up or down the stream only 32 of them would result in the new individual's position being again within the sampled area. As a consequence, 89% of 50 m movements could be, at least in theory, detected with this sampling design. With a specimen's displacement being 500 m long, only 16 out of 36 possible displacements (44.5%) would remain in the sampled area and stand theoretical chance of being recaptured. Therefore, the empirical dispersal rates were corrected to eliminate this bias of observed and theoretically-possible dispersal rates. For example: the observed dispersal rate for 450 m was 1.2% with 50% probability of being detected, results in a theoretical value of 2.4%. In Fig. 3 are shown both, the observed recapture rates and the theoretically-possible recapture rates.

In Table 5, the results of mark and recapture experiments in 18 investigation patches in 1991, which served as a calculation basis for Fig. 3 are shown. In 1991, the greatest observed migration by *C. splendens* along the Schinderbach was a male which covered 1,100 m within 2 days, and a female which flew 950 m in one day. The average distance moved by recaptured banded demoiselles was about 135 m ± 75 m (bias corrected: 189 m ± 77 m). Of the 697 marked damsel-flies that were recaptured (Table 5), 45.2% dispersed less than 50 m, 40.9% between 50 m and 150 m, 7.2% between 150 m and 300 m and 7.7% more than 300 m from the release point. In 1992, the maximum migration distances for *C. splendens* along the Schinderbach were 1.7 and 1.2 km (2 males) and 1.3 km

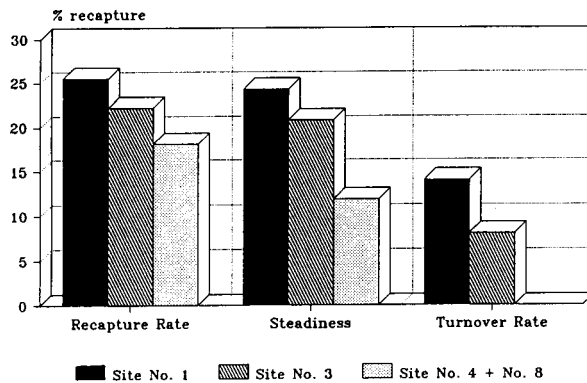


Fig 4. Average values for recapture rates, steadiness and daily turnover rate of the demoiselle populations at two study sites (No. 1 and 3) along the Schinderbach and the out-of-habitat release experiments in investigation sites Nos 4 and 8 during 1991 and 1992.

recapture rates and steadiness of marked damselflies in 1991 and 1992 were calculated. The arithmetic mean of the average recapture rate in Straß and Pfaffing was 23.7% (s.d. = $\pm 3.5\%$). This meant that about 76% of the marked damselflies were not recaptured. In Straß, the recapture rate was about 3% higher than in Pfaffing. Similarly, the average steadiness rates over a period of 10 days varied around an arithmetic mean of 22.5% (s.d. = $\pm 2.5\%$). The average turnover rate in both areas was 14% and 8% for Straß and Pfaffing respectively. The arithmetic mean for both years and areas was calculated. This indicated that 11% of the population disappeared during the mark and recapture experiments from day_n to day_{n+1}.

Forty-nine of the 270 damselflies released outside their habitat areas were recaptured. This is equivalent to a mean recapture rate of 18.1% (Fig. 4). Release and recapture rates for both damselfly species are summarized in Table 5. Fig. 5 shows the percentages of damselflies that were recaptured from the out-of-habitat release points, as a function of distance from the target patch.

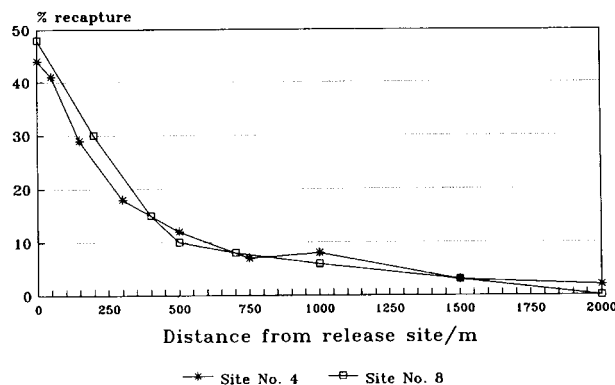


Fig. 5. Observed recapture frequencies at a target patch habitat of *Calopteryx splendens* (Site No. 4) and *Calopteryx virgo* (Site No. 8) released at various distances from it.

(female). A sex-specific bias in recapture rates was observed. In 1991, female-banded demoiselles had a significantly ($p < 0.001$) lower relative recapture rate (15.3%, s.d. = $\pm 8.5\%$) than males (34.3%, s.d. = $\pm 6\%$). In 1992, the recapture rates were similar to 1991, with a rate of 15.8% (s.d. = $\pm 6.9\%$) for females and 31.3% (s.d. = $\pm 5.8\%$) for males, with a significant difference of $p < 0.01$.

To estimate the site attachment of the damselflies (Fig. 4), the average values for recapture rates and steadiness of marked damselflies in 1991 and 1992 were calculated.

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TABLE 6. Distribution of released and recaptured *Calopteryx splendens* and *Calopteryx virgo* during out-of-habitat release experiments for investigation sites No. 4 and No. 8. Release and recapture rates are ranked by sex (male/female).

	<i>Calopteryx splendens</i>	<i>Calopteryx virgo</i>
Released	142/48	47/33
Recapture (day 1)	14/4	7/4
Recapture (day 2)	9/3	0/1
Recapture (day 3–10)	6/1	0/0
Recapture (total)	29/8	7/5

the total recapture to 3.6 : 1. The ratio of male to female beautiful demoiselles was 1.4 : 1 for the released and recaptured groups.

It were male damsel-flies which developed steadiness at the newly colonised brooks. The steadiness of released *C. splendens*, which reached the target patch Roßgraben varied around 11% over a period of ten days. Marked damsel-flies could be recaptured until over two weeks after the release day. For *C. virgo* at the Kuhbacherl, the steadiness rate for a period of three days was 12.8%. Steadiness in such a short time scale was exceptional. In other extra-habitat release experiments with *C. virgo* the steadiness rates fluctuated around 13% for 10 days. During the extra-habitat release experiments, the average steadiness rate for banded or beautiful demoiselles never exceeded 15%. The arithmetical mean steadiness rate for the out-of-habitat release experiments was 11.9% (Fig. 4). In combination with the average recapture rate of damsel-flies during the release experiments, the estimated proportion of released damsel-flies which established some form of steadiness after successfully reaching the target patch, ranged from 3–5%.

Fifty-nine percent of the 49 recaptures of both damsel-fly species were made on the first day after release. For *C. splendens* the recapture rates for the 10 consecutive recapture days declined slowly (Table 6). The sharp decline of recapture rate for *C. virgo* at investigation site (8) after the first day of recapture can be explained. About 10% of the released *C. virgo* were found by the Sur stream, during an 8-day period after release. This stream is situated near the investigation area (8) separated by a street and a distance of about 1,000 m from the target patch Kuhbacherl. The Sur stream was already colonised with damsel-flies of both species.

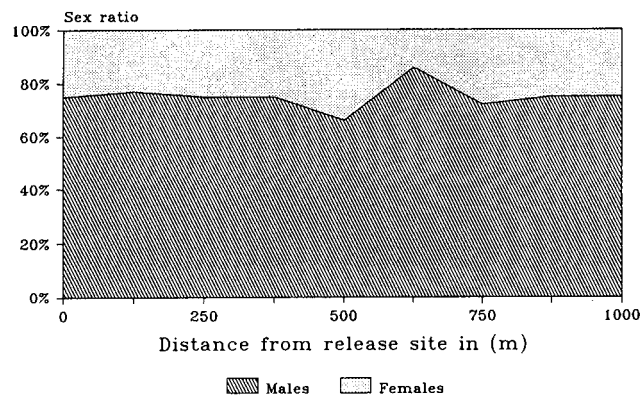


Fig 6. Mean sex ratio at various distances during out-of-habitat release experiments, calculated as the arithmetic mean of all recaptures.

damsel-flies of both species.

A similar observation was made during an extra-habitat release experiment near the Schinderbach valley. To test colonisation behaviour under unfavourable conditions 60 and 27 banded demoiselles were released at the Steinbacherl in 1991 and 1992 respectively. This is a small stream with intensively

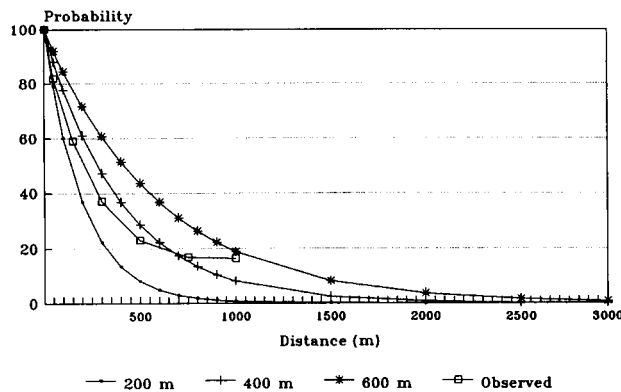


Fig. 7. Observed and predicted migration rates for *Calopteryx splendens* and *Calopteryx virgo* as a negative exponential function of distance ($I = e^{-D/D}$) with species-specific dispersal values between 200 m and 600 m.

bacherl. One day later, investigations of the patch at the Schinderbach, where the damselflies for this experiment were captured, showed a surprising result. Thirty percent of the male and 20% of the female damselflies had returned over a distance of 500 m from the release point at Steinbacherl to their original patch at Schinderbach. A railway embankment (10 m high) separates the two streams spatially and visually. Males and females could be found in their territories, exactly where they had been captured two days previously.

The greatest distance covered was 4 km within 24 h during the extra-habitat release experiments between the two investigation sites No. 4 and No. 8 by a male *C. virgo*. The average distance moved by individuals of both *C. splendens* and *C. virgo* during extra-habitat release experiments at site No. 4 and site No. 8 was about $350 \text{ m} \pm 130 \text{ m}$ (Fig. 5). The average distance during other extra-habitat release experiments rarely exceeded 600 m. Recapture rates of individuals that covered more than 1,000 m ranged between 3–5%. The mean values for sex ratios for all extra-habitat release experiments are shown in Fig. 6. The sex ratio for the release sites was 3 to 1 with 0.75 males and 0.25 females. No significant differences for a sex-specific bias in migration behaviour for the extra-habitat release experiments was found.

DISCUSSION

An area of an appropriate habitat, at least equal to the territory size of one pair is required for a species to maintain even the smallest breeding unit and hence reproduce (Diamond, 1978). A potential habitat must therefore be of a species specific minimum size, below which the patch could not support a population (McArthur & Wilson, 1967). In addition, each species has its characteristic habitat requirements. The likelihood that any given habitat type will be encountered on a census plot increases with the plot's area (Diamond, 1978). The greater an area, the higher the probability that certain species-specific habitat requirements are fulfilled.

used hay meadows as contact areas. In 1991, 7 of the 60 released damselflies were recaptured in the following 3 days at the release point and 12 damselflies were found in neighbouring areas, already inhabited by banded demoiselles. One female was recaptured at her original patch at the Schinderbach, about 950 m distant from the release point. In 1992 on the day after release, no damselflies were observed at the Stein-

The habitat-quality analysis produced a relatively predictable picture of those variables which were important for *C. splendens* and *C. virgo*. There was a strong correlation between their distribution and several habitat quality variables, which fell into three main groups. These were the aquatic habitat, which provided space for the larvae and was characterised by the structure, width and quality of the brook. Secondly, the quality of the terrestrial part of the habitat, which is inhabited by the adults. This was quantified in terms of the quality of contact areas, shading, average vegetation height and density, further light and nitrogen indices. Thirdly, the degree of isolation, which is related directly to the migration ability of the damselflies. For patchily distributed insects, the linkage of populations, via between habitat migration, is essential for the survival of small peripheral populations. This is borne out by the fact that small streams of comparatively poor quality were colonised only temporarily, if there were nearby large and stable populations, e.g., the demoiselle colonies at the Schinderbach. In summary, it is only those habitats that are good enough in quality, and close enough to stable populations (Harrison et al., 1988) that will be inhabited by either *C. splendens* or *C. virgo*.

The correlation between habitat quality criteria and appearance of dragon- or damselflies has been recorded previously. Parr (1973) found that the population density of *Ischnura elegans* (Van der Linden) depended on the vegetation quality. Additionally, the pond size was also related to population density. Zahner (1960) reported a similar phenomenon for *C. splendens*. Zahner (1960) concluded that a stream was only acceptable to demoiselles if it was 40 cm to 60 cm wide.

Prevailing weather conditions, e.g., rain, wind speed and daytime temperatures influence the demoiselles activity quite considerably and, therefore, have a significant effect on the colonisation behaviour and the acceptance of new habitats. Severe climatic conditions, e.g., thunderstorms with strong winds and heavy rain resulted in an increase in mortality of up to 50% (recorded in patch N and O during July 1991). This is enormous in comparison with a daily average mortality rate of 5% during good weather conditions. Similar observations of climatic influence on mortality in butterfly populations were made by Harrison et al. (1988) and Watt et al. (1977). Anthropogenic effects can also influence population demography, for example the reaping of a habitat patch resulted in almost complete emigration of a population of *C. splendens*. Similar observations of the effects of reaping of habitats were made by Zahner (1960) and Pajunen (1966). It is likely, therefore, that the combination of poor habitat quality and severe climatic conditions may result in the local extinction of a small population.

Dispersal behaviour

C. splendens and *C. virgo* tended to migrate over short distances. The results of the mark and recapture experiments in the Schinderbach valley indicated that both demoiselle species are poor dispersers. Similarly, Zahner (1960) found that most *C. splendens* and *C. virgo* migrated between 10 to 200 m, with only 3% migrating over 400 m. Pajunen (1966), Walter (1968), Klötzli (1971) and Waage (1972) also recaptured most individuals near to the release site in studies with migrating demoiselle species. Fuhrmann (1990) found 70% of marked individuals of *C. splendens* not more than 30 m away from the release site and 90% less than 200 m away. Generally, most dispersal observations have shown that the

actual movement of individuals over distances was much smaller than that of which individuals are capable (Slatkin, 1985).

These results indicate that suitable habitat patches for the banded and beautiful demoiselle remain unoccupied, if they are too far from a source of colonists. Similarly Utzeri et al. (1984) found that although dispersal of the damsel-fly *Lestes barbarus* (F.) occurs, it happens so rarely that colonisation of uninhabited ponds is seldom achieved.

Occasional migration by some damsel-flies must occur, since many isolated streams are colonised. These rare migration events are clearly sufficient. The long migration distances observed during this study may explain this phenomenon, which has been noted by other workers. Ott (1987), Eislöffel (1989) and Didion & Handke (1989) found that *C. splendens* or *C. virgo* are well able to emigrate several kilometres. Fuhrmann (1990) found two *C. splendens* individuals 2 km away from their release site, Landmann (1985) and Schmidt (1986) observed demoiselles 1 to 3 km away from suitable breeding sites. Kiauta (1963) recorded *C. virgo* at a glacier lake 11 km away from the nearest population.

The dispersal movements of *C. splendens* and *C. virgo* can be classified according to Danthanarayana (1986):

1. Home range flights or non-migratory movements involve flights within the habitat. For *C. splendens* and *C. virgo*, the range of such flights includes distances up to several hundred meters. Non-migratory movements include activities as feeding, mating, oviposition, territorial flights and movements from the sleeping places to the stream and back.

2. Migratory movements across the landscape facilitate the colonisation of new habitats, recolonisation of old habitats and supplement weak populations at low densities. This study shows that demoiselles could cover several kilometres within a 24 h period. These long-distance flights play an important part in the survival and distribution of a population.

Factors influencing dispersal

It is possible that dispersal behaviour is heterogenous in populations of *C. splendens* and *C. virgo*. Such a heterogeneity has been suggested for the butterfly *Euphydryas editha* by Ehrlich (1961) and for various groups of Diptera by Andrewartha & Birch (1954). It is not known whether demoiselle migratory tendencies are genetically fixed, because little is known about the genetics underlying migratory behaviour (Dingle, 1986). It is not known if migrating behaviour is fixed or is dependent upon the physiological conditions of the individual and upon habitat quality. This study suggests that in habitats of decreasing quality the tendency of the damsel-flies to disperse increases.

There is an apparent negative correlation between the tendency to migrate and population density. Ehrlich et al. (1980) found that for the butterfly *E. editha*, high density was correlated with low migration rates. This negative correlation was partly due to absence of intraspecific competition in these populations. Dobzhansky et al. (1977) found the same inverse relation for *Drosophila pseudoobscura*. His interpretation was that the flies disperse less when they are in favourable habitats than when they are in those unfavourable. This point of view may explain the results for *Calopteryx* in this study, where the average migration distance in an optimal habitat (e.g. No. 1) was 135 m (bias corrected 189 m) and in less favourable habitats (e.g. No. 4 or No. 8 in Fig. 5) was always over 300 m. Additionally, the gregarious tendency of *C. splendens* and *C. virgo* may explain this relationship. Zahner (1960) states that the attachment of *C. splendens* to a certain territory is reduced if

there are no other conspecifics present. Low population densities would raise the individual's tendency to disperse, whereas high population densities result in closer site attachment and steadiness.

Zahner (1960) and Waage (1972) found that the females of both demoiselle species are more mobile than males. No sex-biased dispersal behaviour was observed in this study. There was a significant sex-specific bias in recapture rates for both demoiselle species. But a sex-specific difference in recapture rates cannot be equated with sex-specific difference in dispersal behaviour. Moreover, it is possible that the more conspicuous males were easier to capture than the more camouflaged females and this may have had some influence on this result.

Migration behaviour and distance effects

The degree to which the migration rate coincides with increasing distance from a suitable habitat is of great importance for estimating the chances of a successful colonisation event. This relationship can be described by the negative exponential function:

$$I = e^{-D/D'}$$

where D is the distance from the source to the target patch and D' is a species specific dispersal constant, representing the average distance moved by the species under investigation (Harrison et al., 1988). This formula has both an empirical (Diamond et al., 1976; Gilpin & Diamond, 1976, 1981) and a theoretical (Kitching, 1971) basis. Using a species-specific dispersal constant of 200 m, 400 m and 600 m, a number of curves are generated (Fig. 7). There is an impressive similarity between the hypothetical-calculated and the observed curves of migration rates during out-of-habitat release experiments.

According to the estimated migration probabilities, calculated with the negative exponential function, we can predict the behaviour of a model population. If we assume that the population has a mean dispersal tendency of about 400 m which indicates the empirically determined dispersal rate of *C. splendens* or *C. virgo* during the out-of-habitat release experiments in this study, at a distance of 2,000 m, the dispersal probability would be about 7 damselflies for a population size of 1,000 individuals. For example, the average population size in the main investigation area Straß was about 4,000–5,000 demoiselles. In these calculations, it is assumed that the whole dispersal process occurs from a single point without any stepping-stone effects. The average migration tendencies refer to a time scale of only 24 h. Over a period of several days, via step-by-step dispersal, the possibilities for dispersal could increase significantly. The field experiments imply that the decrease in migration rate for distances over 1,000 m is not as fast as described by the negative exponential model.

The estimations are made on the basis of data from 20–25% recaptured damselflies. Given 100% recapture, the migration rate would be much higher, because the remaining 75% may have included a high proportion of long-range migrators. It can be assumed that, as a consequence of methodical limits, only a small fraction of long-range migrations were detected. Therefore, the real migration rate would be higher than that observed. An approach to this problem is shown in Fig. 3, with a corrected rate of dispersal movements resulting in a more than 1/3 higher average dispersal distance. In addition, per capita rates of migration of the banded and the beautiful demoiselle, appear to be higher with lower population size. The same inverse relationship was observed by Gilbert & Singer (1973)

for the Bay Checkerspot butterfly. This would shift the migration capability of small populations over the estimation levels shown in Fig. 7. Finally it must be noted that all observed individual movements are always minimum calculations, as they reflect the shortest distance between release and recapture points.

The fate of those demoiselles which were not recaptured after marking is unknown. During observation of marked individuals, no serious change in the behaviour of *C. splendens* and *C. virgo* could be detected. Therefore it seems unlikely that they are affected significantly in their migration behaviour by the process of mark and recapture. It is more likely that some of them either moved out of the investigation area or simply died. Lindeboom (pers. com.) describes a type of sub-lethal capture syndrome for both demoiselle species. Capturing the insects with the handnet, resulted in microinjuries of the very delicate zone between caput and prothorax. Immediately after release the damsel-flies showed normal behaviour without any abnormalities in flight or coordination, but the injuries resulted in death one or two days later. Lindeboom (pers. com.) estimated the mortality rate due to this syndrome at about 10% of the capture rate. This would fall within the range for the values of 8 to 14% for this study. Another explanation for the low recapture rates could be the high population densities in the main investigation area. An estimated 5,000 individuals were found along the Schinderbach at one time, making accurate recording of all individuals impossible.

In contrast to Waage (1972), who found that *Calopteryx maculata* (Beauvois) dispersed primarily along the stream course, this study with *C. splendens* and *C. virgo*, showed no evidence for an orientated migratory flight along the stream. Similarly, the downstream movement reported by Zahner (1960) for *C. splendens* was not apparent. Garrison (1978), found that the stream flow had little or no deterministic effect on the movements of *Enallagma cyathigerum* (Charpentier), similar to the observations of *C. splendens* or *C. virgo* in the Schinderbach valley.

In summary, colonisation process is more than just a process of dispersal. The probability of founding a new colony after immigration into a suitable habitat is influenced by many criteria. In accordance with other studies (Harrison, 1989), the reported results indicated after propagule size (Crowell, 1973) as a function of the number of migratory individuals, patch characteristics (Schoener, 1983) and species-specific migration behaviour as the main factors influencing the colonisation process. Species with relative low dispersal ability tend to form metapopulations with more or less distinct local populations. Observed local extinction of demoiselle populations, combined with the process of dispersal and colonisation of new habitats can lead to the conclusion that *C. splendens* and *C. virgo* persist as metapopulations. It became evident that even poor dispersers like the demoiselles in this study are able to recruit enough migrators for successful colonisation.

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