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Short-range dispersal of the Southern Damselfly (*Coenagrion mercuriale*, Odonata) defined experimentally using UV fluorescent ink

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Individuals of the damselfly species *Coenagrion mercuriale* were marked with numbers and with a dot of UV fluorescent ink. Nightly controls with a portable UV-lamp allowed high recapture rates. Only few individuals, however, were recaptured in study sites different from the ones where they had been marked. The maximum distance covered by an individual was 300 m. For nature conservancy issues, this means that protective measures with the aim of preventing further habitat fragmentation are of extreme importance for *C. mercuriale* as one of the most endangered Odonata species of Central Europe.

Key words: *Coenagrion mercuriale*, Odonata, mark-recapture-experiment, dispersal, sex ratio, habitat fragmentation.

Introduction

In the setting of our highly fragmented landscape, there is a strong tendency toward finding a better understanding for the rate of exchange of individuals among local populations which are more or less isolated from one another (e.g., Settele et al. 1996, Amler et al. 1999). However, knowledge about the dispersal ability of most species – and, to an even higher degree, invertebrate species – is insufficient. This inadequacy is in part due to the lack of suitable experimental methods. We tested a method of marking individuals of *Coenagrion mercuriale* with UV fluorescent ink and searching the marked animals at night using a portable UV-lamp. *Coenagrion mercuriale* is a damselfly which is a „species of common interest" protected under annex II of the Habitat Directive of the European law (Rat der Europäischen Union 1992, 1997).

Good recapture rates by the employment of small reflective tags and nocturnal search with a flashlight have been reported for different taxa, e.g. chilopods, grasshoppers and isopods (Mühlenberg 1993). Reflective paint with minute glass beads was successfully used for the same purpose (Youdeowei & Service 1983). UV fluorescent powder helped to determine nighttime resting sites of *Drosophila* (Begon 1978; Begon et al. 1975; Crumpacker 1974) and tsetse flies (Youdeowei & Service 1983). The experiment's most important aim was to obtain data about the intensity of exchange of individuals from different study sites within the study area.

Study area and methods

The study area is situated in southwestern Germany close to the city of Freiburg i. Br. It consists of areas of arable land and meadowland and is enclosed by forest on three sides. In a small area of 41.5 ha, there are two ground water ditches (D = Dierlochgraben and E = Ettenbach) and one brook (H = Hanfreezbach) with a total length of 1,095 meters which are colonised by *Coenagrion mercuriale*. The ditches were subdivided into several sections referred to as „study sites" (Fig. 2). The water of sections D1 through D3 and E1 through E5 flows northwards, and of sections H and E6 westwards. Weather conditions during the investigation period changed between sunny days with high flight, mating, and oviposition activities and days with less favourable conditions.

Between May 22 and 24, 2000, a total of 395 individuals (both adult and subadult ones) were marked with the UV-pen „edding securitas uv marker". A small dot with a square of a few mm on one wing is sufficient for safe relocation. The fluorescent ink is almost invisible in daylight and displays a blueish-white glow under UV light. It dries fast and it is permanent and waterproof. The animals were also marked individually on one wing with three-digit numbers using permanent overhead projector pens (Staedtler Lumocolor transparent S). It is recommended to first write the numbers on a hind wing, let dry

and then apply the UV-ink. This procedure inhibits running of the numbers and allows the animals to take off right after marking, reducing the risk of their wings sticking together. For all marked animals, date of marking, sex, and study site were noted. A portable UV-lamp was built by equipping a small neon lamp powered by a 12 V lead akku with UV fluorescent tubes (black light). Light-coloured plastic parts in the reflector of the lamp were covered with black paper to avoid the emission of diffuse light. A shade helped deflect light that could blind the observer. Detailed information on our method can be found under
http://www.inula.de/extras.html.
Following the marking, nightly observations were carried out on May 23 and 24, May 26, 27, and 28, and June 17 and 18, 2000. The study sites themselves as well as the adjacent area were searched for marked individuals. A stripe of approximately 8 m was illuminated, animals resting in exposed positions could be located at a distance of more than 10 m. Forest edges close to the study sites and linear structures such as grassy waysides and strips of vegetation along dried-up ditches were searched as well. For each recaptured individual, number, study site, and distance from the water were noted.

Results

1. Recapture rates and sex ratio

Out of 395 marked individuals, a total of 140 (35%) were recaptured at least once (116 specimens once, 19 specimens twice, and 5 individuals three times). The longest life span found between sightings was six days.
The sex ratio of marked animals was 337 males (85%) to 58 females (15%). Thirtyfour percent of the marked males and 41% of the marked females were recaptured at least once (Table 1). According to the χ^2-test (Zöfl 1992) these differences in recapture rates are not statistically significant.
Over the course of the study, a clear change in sex-specific recapture rates was noted: On the first three dates, the recapture rates of males and females did not differ significantly. During the last successful nightly observations on May 28, 2000, however, 11 % of all marked males, but only 3% of all marked females were recaptured. This difference in sex-specific recapture rates is highly significant ($\chi^2 = 13.89$, $p \leq 0.1$). Two nightly controls carried out some time later, on June 17 and 18, 2000, were unsuccessful: no marked individuals were found. Table 2 shows the number of individuals that had been marked up to a given control session, and the corresponding sex ratio (which ranges from 84 to 85% males and is thus almost constant). For each date, the total number of recaptures and the number of recaptured males respectively females is displayed. As some individuals were recaptured on several days, the sum of all recaptures is N = 169.
Two marked males and one marked female were caught as „tandems" (male attached to female) with non-marked partners. Three specimens, two of them two days and one three days after marking, were found in spider webs; their three digit numbers were still legible.

2. Nighttime resting sites

The damselflies were usually found at a height of approximately 20 cm clinging to blades or stalks of grass or, more seldom, young corn plants. Along forest edges, swales, and other linear structures, no animals were found. Fig. 1 shows the distribution of all 169 individuals recaptured on 10 distance classes. Each distance class is 10 m wide, with the first class representing a 5 m stripe on both sides of the center line of the running waters. Damselflies found here spent the night adjacent to the water; this is where most of them were sighted again. Up to a distance of 25 m, individuals were encountered in much lower densities. At greater distances, only single individuals were found.

3. Short-range dispersal

The individual numbering allowed us to detect the movement of individuals between different study sites (Fig. 2).
A total of 11 individuals were recaptured along sections different from the ones where they had been marked. Ten of them were males. Due to the high percentage of marked males (85%), this finding does not reflect significant differences in sex-specific dispersal behaviour (χ^2-test).
In eight cases, only short minimal distances (between neighbouring sections) could be shown. One individual that moved from section E2 to E4 must have covered a distance of at least 60 m, another one moved

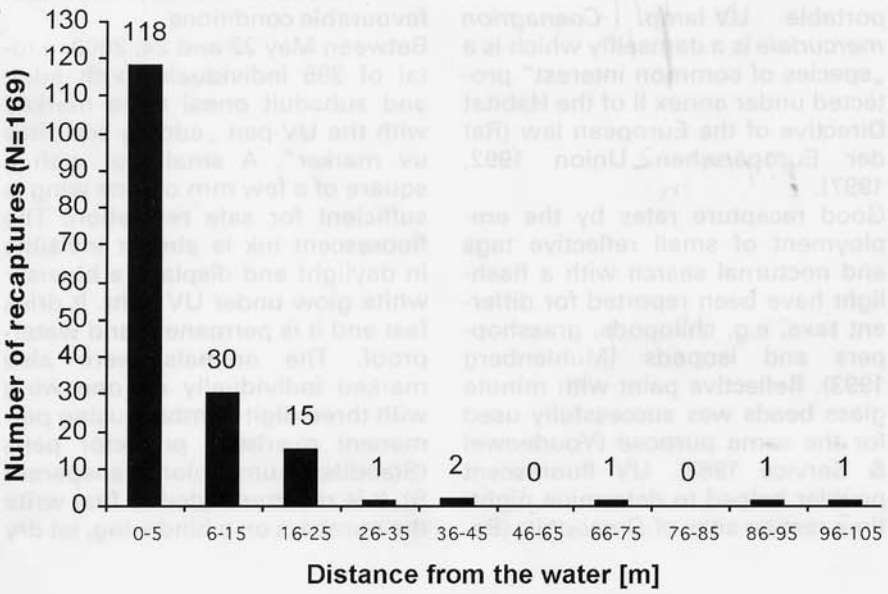

Fig. 1. Distribution of all recaptures on distance classes from the study sites.

Table 1. Number of *Coenagrion mercuriale* marked and recaptured on the study sites. The column „marked individuals" shows the percentage of males versus females. The column „recaptured individuals" displays the percentage of all recaptured individuals, and for males and females respectively.

Study water section	Length (m)	Marked individuals			Recaptured individuals		
		total	males	females	total	males	females
H	75	103	82 (80%)	21 (20%)	41 (40%)	32 (39%)	9 (43%)
E1–E6	610	245	215 (88%)	30 (12%)	67 (27%)	57 (27%)	10 (33%)
D2–D3	410	47	40 (85%)	7 (15%)	32 (68%)	27 (68%)	5 (71%)
Sum	1.095	395	337 (85%)	58 (15%)	140 (35%)	116 (34%)	24 (41%)

Table 2. Recapture rates of males and females of *Coenagrion mercuriale* during different nightly observations.

Date of observation	Sum of marked individuals until date of observation			Number of individuals recaptured on date of observation			Recapture rate of males/ females
	total	males	females	total	males	females	
23.5.2000	66	56 (85%)	10 (15%)	20 (30%)	15 (27%)	5 (50%)	1:1.9
24.5.2000	314	263 (84%)	51 (16%)	72 (23%)	61 (23%)	11 (22%)	1:1.0
26.5.2000	348	293 (84%)	55 (16%)	38 (11%)	30 (10%)	8 (15%)	1:1.4
28.5.2000	395	337 (85%)	58 (15%)	39 (10%)	37 (11%)	2 (3%)	1:0.3
17.0.2000	395	337 (85%)	58 (15%)	0 (0%)	0 (0%)	0 (0%)	
18.6.2000	395	337 (85%)	58 (15%)	0 (0%)	0 (0%)	0 (0%)	

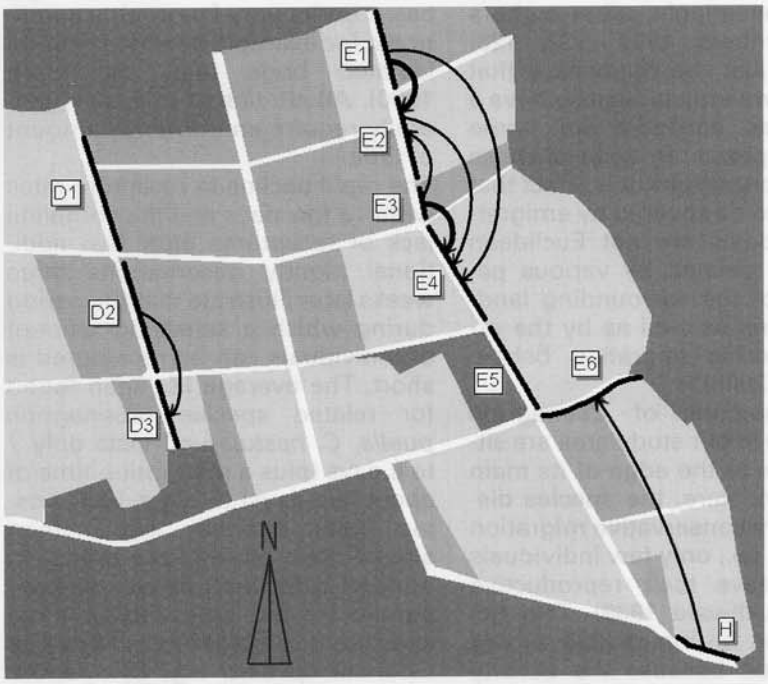

Fig. 2. Study area and movements of individuals between study sites. Light grey = meadowland, medium grey = arable land, dark grey = forest, white = gravel roads, black = study sites. Study site abbreviations: D = Dierlochgraben, E = Ettenbach, H = Hanfreezbach. The arrows indicate movements of damselflies between study sites (thin arrow = one individual, thick arrow = three individuals). Scale: lenght of arrow running from H to E6 approx. 300 m.

at least 170 m from E1 to E4. All of these animals have obviously moved along their „home waters". Nine of them moved upstream and one downstream. The longest distance (≥ 300 m) was covered by an individual which moved from section H to section E6.

Postcript: In 2001, circa 150 individuals were marked at study site H. Two (one male, one female) were recaptured et E6. The longest life span found between sightings was 16 days.

■ Discussion

The method of nightly search for individuals of *Coenagrion mercuriale* marked with UV fluorescent paint has proven to be very successful and is considered more effective than conventional marking methods. It can be assumed that all individuals were recaptured within an approximately 8 m-wide strip illuminated by a portable UV-lamp. The visibility even of small fluorescent marks was very good. A low level of diffuse light (study area outside of settlements) and no or little moon-light are good prerequisites. Advantages of nightly search for marked individuals are first that selectively only marked animals are detected, second that the animals are almost immobile and can easily be recorded, and third that the spatial distribution of the individuals is not affected by the observer's activity. A disadvantage was that the individuals were usually covered with dew, which made it sometimes hard to decipher the individual wing numbers. Fluorescent spider cocoons somewhat interfered with spotting the marked animals. However, the fluorescence of these cocoons was much weaker than that of the fluorescent ink.

In spite of the high total number of recaptures, only a low level of exchange of individuals from different study water sections was found. Recent studies in Great Britain yielded very similar results (Jenkins 2001). The enclosure of the study area by forest on three sides makes it appear likely that an increased number of individuals moves westwards toward the open landscape in order to search for and colonise new waters and thus contribute to dispersal of the species. However, this effect could not be shown. The results indicate that *C. mercuriale* might move preferredly along running water that is used as their reproductive habitat. Individuals showing this behaviour avoid risk of moving away too far from a suitable reproductive habitat. We must not forget, however, that our method does not allow conclusions about the movement patterns during the day. Also, the thinning effect with growing distance from the study sites leads to a strong decrease in recapture probability. The fact that most individuals moved upstream might possibly be explained by a phenomenon called „upstream oviposition flight." Many stream-inhabiting insect taxa are known to move this way before oviposition in order to compensate for territorial loss due to larval drift (e.g., Zwick 1990). For broadwinged damsel species (*Calopteryx splendens, C. virgo*), Stettmer (1995, 1996) did not find evidence for a preferred moving direction upstream. In contrast, Zahner (1960) found an increased rate of individuals of the two species named above flying downstream.

The maximum covered distance that was observed (about 300 m) lies most likely within the species' home range. The home range encompasses, among others, resting habitats, feeding habitats, and reproductive habitats between which an individual switches daily without actually moving away from its reproductive habitat.

A function of linear structures other than water-filled ditches, e.g. forest edges, wayside vegetation, swales, vegetation along dried-up ditches, as corridors could not be shown. As we pointed out earlier, however, the method employed cannot give direct insight into the actual „flight route," but only shows where an individual ends up at the end of the day. Stettmer's results for the *Calopteryx* species (1995, 1996) provided neither evidence for a movement along the stream nor for a separating effect of potential barriers. Stettmer (1995, 1996) does not only define forests and arable lands as such potential barriers but also streets and railway enbankments. Interestingly, other authors (e.g., Sternberg 1999: 122, 126) point out just the opposite – that the latter two structures may have a function as corridors for some Odonata species. In spite of these contradictory results, it is a fact that distances to be covered by emigrating individuals are not Euclidean but rather defined by various parameters of the surrounding landscape matrix as well as by the organism-specific migration behaviour (Lang 2000).

The populations of *Coenagrion mercuriale* in our study area are situated close to the edge of its main distribution. Here, the species displays a very conservative migration behaviour, i.e., only few individuals tend to leave their reproductive habitat (Buchwald 1989). This behaviour can be interpreted as risk minimization because the density of suitable habitats decreases toward the edges of its main distribution with the implication that emigrating individuals run a high risk of failing to reach a suitable habitat for reproduction. From the evolutionary and biogeographical point of view, it is a crucial demand that emigration has to take place (Sternberg et al. 1999). Observations of adult *C. mercuriale* in distances of up to 3 km away from the closest known reproductive habitat (Jentzsch & Norgall 1988, our own observations) show that the species is able to cover longer distances. The colonisation of new habitats allows indirect conclusions about long distance dispersal. To what degree these events might be accidental, e.g. caused by wind drift, has still to be considered a „black box".

All in all, the results of this study cast a light on the difficulties encountered when trying to obtain „hard data" required for dispersal models and population viability analyses. Other modern methods of studying movement behaviour of small invertebrates such as the use of harmonic radar (Mascanzoni & Wallin 1986, Janßen & Plachter 1998) are usually expensive, and even modern radio-transmitters are still too heavy to be used for small insects (Riecken & Ries 1992). Long-range dispersal can be investigated only in rare cases under very favourable conditions, for example between several isolated bogs (e.g., Sternberg 1990). All studies of this type generally require an immense amount of time.

The rapid decline in recapture rates within a few days and the complete lack of recaptures after two additional nightly observations three weeks later illustrate that the period during which a satisfying amount of individuals can be recaptured is short. The average life span found for related species (*Coenagrion puella, C. hastulatum*) lasts only 7 to 8 days (plus a maturation time of about five days) (Steiger 1988, Lösing 1988). Basically, our method should have allowed the detection of dead individuals as was demonstrated by the detection of three specimens in spider webs. In some Odonata species, e.g. *Sympetrum danae*, emigration rate increases during maturation and aging (Sternberg & Hunger 2000). Our study does not allow answers for the question whether the marked animals died or emigrated.

The sex ratio of all marked animals of 85% males to 15% females is typical for Odonata in their reproductive habitats. The shift of recapture rates from near equilibrium towards a significantly higher recapture rate of males during the course of the study stresses once again that the females move towards the reproductive habitat merely for the purpose of mating and ovipositioning and leave a few days afterwards. The males, on the other hand, probably spend most of their adult lives close to suitable reproductive habitats in order to increase the likelihood of mating with one of the few females available at any given point of time. Other explanations are possible, e.g., the lower recapture rate of females might be caused by a hypothetical higher female mortality.
In the three observed cases of marked individuals found spending the night as „tandems," the coupled animals stopped their activity near the end of the day. Such males, who managed to seize one of the rare females near the end of the diurnal activity period, will now be able to successfully complete copulation and oviposition the next day.
The spatial distribution of nighttime resting sites shows that the damselflies which concentrate along the ditches and brooks under favourable weather conditions, disperse and use some of the surrounding area at night. This behaviour was shown for other Zygopteran species, too (Sternberg 1994). Buchwald et al. (1989) found similar results for the resting sites of *C. mercuriale* during bad weather.
The results indicate once more that a network of individual-rich occurrences is crucial for the long-term survival of *Coenagrion mercuriale*. *C. mercuriale* is considered one of the rarest Odonata species of Central Europe (Schiess & De Marmels 1979). As a species listed under annex II of the habitat directive (Rat der Europäischen Union 1992, 1997), it is strictly protected by European law. Without protection measures, further fragmentation of its range has to be expected – the few remaining populations of the northern prealpine region are already „probably completely isolated" (Sternberg et al. 1999). Studies of Kiauta & Kiauta (1988) of an isolated population in Liechtenstein demonstrated the possible consequences: Analysing the genetic potential, they found an extremely low recombination index, which is to be interpreted as an increase in fertility at the cost of a decrease in ecological flexibility and adaptation ability. The consequence is a high risk of extinction of this local population following even small changes of its habitat.

Zusammenfassung

In unserer hochgradig fragmentierten Kulturlandschaft ist ein besseres Verständnis über den Individuen- und damit Genaustausch zwischen den oft inselartig verteilten Lokalpopulationen einer Art von großer Wichtigkeit. Die Kenntnisse zum Ausbreitungsverhalten von – insbesondere wirbellosen – Tieren sind indes meist gering, was zu einem großen Teil auf das Fehlen geeigneter experimenteller Methoden zurückgeht. Am Beispiel der europaweit geschützten und in Anhang II der Fauna-Flora-Habitat (FFH)-Richtlinie der EU als Art „von gemeinschaftlichem Interesse" verzeichneten Helm-Azurjungfer (*Coenagrion mercuriale*) wurde eine bisher weitgehend unbekannte Methode der Markierung mit UV-fluoreszierender Farbe und nächtlicher Suche mit einer tragbaren UV-Lampe erprobt.
Die Methode, deren Vor- und Nachteile im Text diskutiert werden, erwies sich als sehr erfolgreich in bezug auf die erreichte Wiederfangrate. Von 395 Exemplaren, die in einem gut 40 ha großen Untersuchungsgebiet mit mehreren von der Art besiedelten Graben- und Bachabschnitten markiert wurden, wurden während der Laufzeit des Versuchs insgesamt 140 Individuen (35%) mindestens einmal wieder gefunden. Die längste nachgewiesene Lebensdauer eines markierten Individuums betrug sechs Tage. Das Verhältnis markierter Männchen zu Weibchen lag bei 337 Männchen (85%) zu 58 Weibchen (15%). Während der ersten Kontrolltermine unterschieden sich die Wiederfangraten von Männchen und Weibchen nicht signifikant, während zum Ende des Versuchs hin mit 11% ein signifikant höherer Anteil markierter Männchen als markierter Weibchen (3%) wieder gefunden wurde.
Insgesamt elf Tiere wurden an einem anderen Gewässerabschnitt als dem, an dem sie markiert wurden, wieder gefunden. In zehn Fällen wurden nur geringe minimal zurückgelegte Distanzen entlang ein- und desselben Gewässers nachgewiesen. Dabei bewegten sich neun Individuen gegen und ein Tier mit der Fließrichtung. Lediglich ein Individuum bewegte sich zu einem 300 m entfernt gelegenen anderen Gewässer.
Die untersuchten Vorkommen liegen am Rand des Hauptareals von *Coenagrion mercuriale*. Die Art ist hier sehr schlüpforttreu, verhält sich also bezüglich ihres Ausbreitungsverhaltens sehr konservativ. Die Ergebnisse unterstreichen den Sonderstatus der Art in Mitteleuropa, die hier zu den am stärksten bedrohten Libellenarten gehört und zu Recht in Anhang II der FFH-Richtlinie verzeichnet ist. Das klare naturschutzfachliche Fazit lautet, dass Schaffung und Erhaltung eines möglichst dichten Netzes individuenstarker Vorkommen zur langfristigen Erhaltung der Helm-Azurjungfer von äußerster Wichtigkeit sind.

Summary

In our highly fragmented cultural landscape, a better understanding of exchange processes of individuals and thus genes among local populations which are distributed in a patchwork manner is of utmost importance. However, knowledge about the dispersal behaviour of most species – and especially invertebrate species – is insufficient. This is in part due to the lack of suitable methods. We tested a method of marking individuals of the southern damselfly (*Coenagrion mercuriale*) with UV fluorescent ink and tracking the marked animals using a portable UV-lamp. *C. mercuriale* is a „species of common interest" protected by the Habitat Directive of the European

law (Rat der Europäischen Union 1992, 1997).

The method – its advantages and disadvantages are discussed in the text – proved to be very successful and allowed high recapture rates. Out of 395 individuals that were marked in a study area of 40 ha comprising several ditch and brook sections colonised by *C. mercuriale*, a total of 140 (35%) were sighted again at least once. The longest life span found between sightings was six days. The sex ratio of marked animals was 337 males (85%) to 58 females (15%). Over the course of the study, a clear change in sex-specific recapture rates was noted: Initially, the recapture rates of males and females did not differ significantly. On later dates, a significantly higher percentage of marked males compared to marked females were sighted again (11%, resp. 3%).

A total of 11 individuals were tracked along sections of study waters different from the ones where they had been marked. In ten cases, only short minimal distances (between neighbouring sections) were covered. Only one individual moved to a different study water at a distance of 300 m.

The populations of *C. mercuriale* in our study area are situated close to the edge of its main distribution. Here, the species displays a very conservative migration behaviour, i.e., only few individuals tend to leave their reproductive habitat.

The results highlight the specific situation of *C. mercuriale* in Central Europe. Here, it is one of the rarest Odonata species and its status as a protected species under annex II of the Habitat Directive is justified. The clear message for nature protection reads: establishing and sustaining a network of individual-rich occurrences is crucial for the long-term survival of *C. mercuriale*.

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