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## Ecological and genetic measurements of dispersal in a threatened dragonfly

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## ABSTRACT

*Leucorrhinia caudalis* is a rare dragonfly, threatened throughout its European distribution. The species was formerly widespread in the Swiss lowlands, but only a single population remained in the 1980s. However, a spread has recently been observed, with additional ponds being colonised, sometimes at considerable distance. Despite this evidence of recent long-distance dispersal, it is unknown whether *L. caudalis* regularly moves among ponds or whether this is a rather rare event. A combination of an ecological mark-resight and a population genetic study was applied to investigate contemporary dispersal and the genetic footprint of the recent population history of *L. caudalis* in Switzerland. DNA for genetic microsatellite analysis was extracted from exuviae. The mark-resight study and the genetic analysis gave congruent results. They showed that *L. caudalis* is mostly a sedentary species, with only a few contemporary dispersal events over distances up to 5 km being observed. The genetic analysis was in agreement with the recent population history of the Swiss populations. The oldest and largest population showed large genetic diversity and acted as source population for the recent spread of *L. caudalis* in Switzerland. Recurrent gene flow among this source population and close populations caused substantial local genetic variation in the latter, as well as low population differentiation. The two recently founded distant populations ( $\geq 30$  km distance) were genetically less diverse and highly differentiated. These distant populations and another recently colonised population also expressed signatures of genetic bottlenecks.

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## 1. Introduction

Many formerly widespread dragonfly species suffered a severe decline in Europe during the last decades, both in numbers of populations and individuals. Dragonflies depend on water bodies for their reproductive cycle and are therefore strongly affected by the loss of ponds and wetlands or the regulation of rivers and streams. In addition to habitat loss (Fahrig, 2003), landscape fragmentation causes the decline or local extinction of dragonfly populations (Watts et al., 2004, 2006). Remaining populations are often small, spatially isolated and decreasing in size. However, many water bodies are now protected, and a positive trend of population stabilisation has been observed in several dragonfly species, some species even colonising new or restored habitats (Kadoya et al., 2004). Such colonising processes are highly dependent on the dispersal ability of species.

If dispersal results in successful mating and reproduction in a new population, dispersal translates into gene flow (Allendorf and Luikart, 2007). Gene flow links populations and prevents genetic drift and inbreeding. In dragonflies, non-trivial flights can be assigned to four types, some of them potentially leading to dis-

persal and gene flow (Corbet, 1999): (1) maiden flights to the first resting site just after emergence, (2) commuting flights, practiced daily between the roosting site and the reproductive and foraging sites, (3) seasonal-refuge flights between the emergence site and a refuge site with better conditions for foraging and maturation (only known from Mediterranean countries) and (4) migration that only occurs once per generation, covering longer distances.

Demographic or genetic information on the dispersal ability of dragonflies in fragmented landscapes is often not available. Such knowledge is, however, important to judge upon the impact of fragmentation on populations, to decide whether conservation measures have to be taken and to evaluate whether corresponding measures are successful (O'Brien, 1994; Angelone and Holderegger, 2009). While the life cycle characteristics, ecological demands and geographical distribution of many odonate species are well described (Sternberg and Buchwald, 1999, 2000), little is known about their dispersal ability or population dynamics. Dispersal capacity greatly influences the survival and the population dynamics of species in today's fragmented landscapes. An example of a rare damselfly whose dispersal ability has carefully been studied is *Coenagrion mercuriale* in southern England. This sedentary species has limited dispersal capability, with more than 75% of marked individuals moving less than 100 m (Watts et al., 2007) and inter-population dispersal being very rare (3.4%; Rouquette and Thompson, 2007).

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For measuring contemporary dispersal, both ecological and genetic methods can be applied (Clobert, 2001). Ecological approaches usually track marked dragonfly individuals in mark-recapture field studies. The disadvantage of this approach is the probability of missing long-distance or periodic dispersal events. These drawbacks can be overcome by using population genetic methods enabling the estimation of current migration at the landscape level (Manel et al., 2005; Holderegger and Wagner, 2008). A combination of both ecological and genetic methods thus covers most aspects of dispersal in dragonflies. However, these methods have rarely been applied in concert (but see Watts et al., 2004, 2007).

In the present study, we investigated the rare dragonfly *Leucorrhinia caudalis*, a species threatened throughout its European distribution (Sternberg et al., 2000). In Switzerland, it is categorized as endangered on the Swiss Red List (Gonseth and Monnerat, 2002). In 1980, the species was only known from a single remaining population in the Swiss Canton of Aargau (Vonwil, 2005). In the 1990s and 2000s, new colonisations of nearby ponds, that had been newly created or were restored, occurred. Distances between these newly colonised ponds and the remnant probable source population ranged from 500 m to 7 km. Surprisingly, recent long-distance colonisation also happened at distances of 30–50 km in the 2000s. At present, there are six larger and three small, not permanently occupied populations of *L. caudalis* in Switzerland (Table 1). While the above colonisation history clearly shows that long-distance dispersal occurs in *L. caudalis*, nothing is known about contemporary dispersal rates. It is thus unknown, whether inter-population dispersal is rare or occurs on a regular basis.

Based on detailed monitoring data (Vonwil and Osterwalder, 2006), the present article investigated the current dispersal capacity of *L. caudalis* in a combined ecological (mark-resight method; Purse et al., 2003) and genetic (first generation migrant assignment tests; Paetkau et al., 2004) study. We examined dispersal rates and distances among more closely located ponds ( $\leq 7$  km) as well as among geographically isolated sites ( $\leq 50$  km distance). Furthermore, we checked whether the recent colonisation history in Switzerland led to detectable genetic bottlenecks or founder effects in populations of *L. caudalis*.

## 2. Materials and methods

### 2.1. Study species

*L. caudalis* (Charpentier, 1840, Libellulidae) is a spring dragonfly emerging at the beginning of May and having a peak flight season from mid-May to mid-June (Vonwil, 2005). Adult males spend most of their lifetime at ponds, while females only return to ponds

for mating and egg laying. Larvae hatch 2–6 weeks after oviposition and overwinter in submerged vegetation, where they stay until their 1 or 2 year larval development is completed (Sternberg et al., 2000; Mikolajewski et al., 2004). Although *L. caudalis* is supposed to be a weak flier, individuals have been observed at distances of 5–10 km from ponds (Vonwil, 2005).

The distribution of *L. caudalis* ranges from France to southern Scandinavia and western Siberia. The main distribution area is located in eastern Germany, southern Finland and Poland. The geographically closest populations to those in Switzerland are in southern Germany and eastern France (Vonwil, 2005). Across its whole distribution range, populations of *L. caudalis* have declined and most remaining populations are spatially isolated. Thus, *L. caudalis* is threatened throughout Europe (Sahlén et al., 2004). Main causes are intensive fishing, environmental pollution and decline of submerged and floating vegetation, caused by changes in water chemistry and thermal cycling as well as increasing water turbidity (Sternberg et al., 2000).

In the Swiss lowlands, the species was formerly widespread, but during the 1980's, all known populations except a single one were extinct (population SRB; Table 1, Fig. 1). Over the last two decades, a spread of *L. caudalis* has been observed (Vonwil, 2005) and several ponds in the Cantons of Aargau, Zurich and Thurgau were newly colonised (Table 1). This development mainly occurred due to the creation and restoring of ponds in the Canton of Aargau. The reasons for the establishment of the distant populations in the Cantons of Zurich and Thurgau remain unclear. In Germany, Mauersberger (2009) assumed that global warming was a probable cause for the increase of *L. caudalis* populations.

### 2.2. Mark-resight study

We carried out a mark-resight study in the Canton of Aargau in 2008 (Fig. 1), including all locations of *L. caudalis* in Switzerland except for two distant locations in the Canton of Zurich and Thurgau. A total of 516 mature individuals (456 males and 60 females) were caught with an insect net at three sites: Stille Reuss (SRB), Birriweiher (BW) and Unterrütiweiher (UW; for sample sizes see Table 1). Mass emerging of *L. caudalis* started on May 6 at site SRB and a few days later at sites BW and UW. After emergence, imagines left the ponds and returned approximately 1 week later. Adults were then caught from May 13 to 16 and May 27 to 30. Each insect was individually marked by putting one to eight colour stripes (nail polish diluted with acetone 1:5) at eight different wing positions (Flöss, 1998; Knaus and Wildermuth, 2002). Colours on front wings identified the pond where individuals were marked. This enabled the unequivocal identification of individuals, which had moved from one pond to another.

**Table 1**

The eleven current populations of *Leucorrhinia caudalis* in Switzerland. Given are the location, abbreviation, census population size in 2008 (Vonwil, unpubl. data), the year of colonisation and the sample size of the mark-resight study ( $N_{mr}$ ) and the genetic analysis ( $N_{genetic}$ ). Note that five populations are small and not permanently occupied (\* not occupied in 2008).

Canton	Location	Abbreviation	Population size in 2008	Year	$N_{mr}$	$N_{genetic}$
Aargau	Fischbachermoos	FM	30	1991	–	4
	Cholmoos	CM	*	<1988	–	–
	Steinenmoos	StM	*	2000	–	–
	Stille Reuss	SRB	9000	<1988	249	48
	Obersee	OS	<20	2000	–	–
	Seematten	SM	<20	1993	–	–
	Birriweiher	BW	600	1998	165	30
	Unterrütiweiher	UW	800	2006	102	31
	Schorengrindel	SG	<20	2003	–	–
Thurgau	Pfyn	TG	430	2004	–	33
Zurich	Dätt nau	ZH	350	2004	–	44

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