Development of two common dragonfly species with diverging occupancy trends

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Abstract
The two sibling and syntopic odonate species Sympetrum striolatum and Sympetrum vulgatum are common and widespread in Central Europe. While S. striolatum has strong positive population trends, declines of S. vulgatum are observed. The aim of this study was to identify possible drivers of these diverging trends. We presumed that differences in egg development may lead to differences in survival until hatching. First, eggs laid in non-permanent or shrinking waterbodies may suffer of increasing drought periods. Second, differences in development may cause increased size-mediated intraguild predation, a common cause of reduced survival in odonate larvae. Egg development time and hatching rates were recorded of eleven egg clutches of S. vulgatum and ten clutches of S. striolatum under simulated drought vs. water and direct vs. delayed development treatments. Hatching rates were reduced under drought conditions, and particularly so in S. vulgatum. We did not observe obligate winter diapause in any of the egg clutches. But, S. vulgatum varied widely in development between clutches, while the eggs of S. striolatum developed much faster and hatched highly synchronously. This would provide S. striolatum with a temporal advantage that may lead to a size-advantage over most S. vulgatum. We also found that S. vulgatum grew faster. Faster larval growth would only compensate for those S. vulgatum with fast egg development. The current population trends may be partly attributed to lowered survival of S. vulgatum under drought and by phenological and, thus, size benefits of S. striolatum.

Implications for insect conservation Our results show that population dynamics of two closely related dragonfly species can be explained by climatically induced changes in their interactions. Understanding the causes and processes of behavioural changes resulting in differing population trends is fundamental for the protection of species.

Keywords Climate change · Egg development · Intraguild predation · Larval growth · Mortality · Phenological shifts

Introduction
Insect conservation often concentrates on charismatic or threatened species, while the population trends of common and widespread species remain unnoticed (Gaston 2011). Nevertheless, recent studies provide evidence of decline of common species, for instance of Lepidoptera (Habel and Schmitt 2018; Kurze et al. 2018; Salcido et al. 2020) and Coleoptera (Losey et al. 2007; Homburg et al. 2019). Since numerical declines of common and widespread species may impact the composition and functioning of ecosystems more severely than the declines of rare species (Cardoso et al. 2020) they need to be specifically addressed. The drivers of insect decline are manifold, among them habitat loss, pollution, invasive species, and climate change (Cardoso et al. 2020). Aquatic insects are supposed to be disproportionately affected by climate change, due to the synergistic negative effects of other factors on freshwater ecosystems (e.g. eutrophication, acidification, salinization) overall (Woodward et al. 2010; Reid et al. 2019).

Anthropogenic climate change has been shown to have a large impact on species abundance, distribution, development, and phenology (Parmesan et al. 1999; Parmesan 2006; Robinet and Roques 2010; Chen et al. 2011; Devictor et al. 2012; Halsch et al. 2021). Particularly warming may affect species and communities in different ways. For instance, receding water levels with progressing drought...
may expose freshwater organisms to adverse conditions (Bond et al. 2008). In ectotherms, temperature has a significant impact on the metabolic rate (Gillooly et al. 2001), which in turn influence for example growth and development (Angilletta et al. 2003). Since ectotherms may differ in their specific response of growth to temperature (Angilletta Jr et al. 2004) the future warming scenario effect can differ between species. In addition, due to species-specific differences in development, warming may cause asymmetric shifts in phenology, which then may trigger temporal mismatch between interacting members of communities (Cushing 1969; Kharouba and Wolkovich 2020). For instance, asymmetric shifts of seasonal appearance between prey and predator have been reported to cause reduction in foraging and by that in reproduction success (Both et al. 2009). Also, the types of interactions between species may be altered via size-mediated interactions between intraguild predation and competition (Yang and Rudolf 2010; Rudolf 2019) and priority in colonization (Fukami 2015). In addition, climate-induced range expansions may cause or intensify contact between ecologically similar species and introduce high levels of interspecific competition and intraguild predation to populations already stressed by changing climatic conditions (Urban et al. 2012). Establishment of—climate driven—invaders may impose negative effects on the native species due to their interaction with the invasive species (Tylianakis et al. 2008), and these negative effects could be strengthened by difference in temperature reactions between the native and invasive species (Suhling and Suhling 2013).

Dragonflies are intermediate or top predators in freshwater ecosystems and provide a critical link between freshwater and terrestrial communities (Knight et al. 2005). As a result, the effects of climate change on dragonflies may extend beyond the freshwater environment and have the potential to alter processes across ecosystem boundaries (McCauley et al. 2015). Dragonflies species respond to warming in various ways (Hassall and Thompson 2008), such as poleward range expansion (Aoki 1997; Hickling et al. 2005; Ott 2010) and changes in phenology (Hassall et al. 2007). While it seems that some species profit by increasing site occupancy others exhibit negative trends (Termaat et al. 2019; Bowler et al. 2021), and consequently communities change (Flenner and Sahlén 2008). Still, the ultimate causes for changes are often unknown. There may be direct adverse responses to high temperature or drying since there are species-specific and often also stage-specific reactions and requirements. Also differences in the development may lead to size-mediated intraguild predation (Rasmussen et al. 2014).

Dragonfly development is affected by internal and external factors (Pritchard et al. 1996; Corbet et al. 2006). An internal factor governing the development is seasonal regulation, which is triggered mainly by daylength variations review in (Norling 2021). Embryonic development may be direct or triggered by various types of diapause (Ando 1952). External factors are food availability and temperature which directly affect growth (Corbet et al. 2006). The development response to temperature seems to be species-specific (Suhling et al. 2015). Rapidly growing larvae gain size advantages, which, in turn, may cause size-mediated intraguild predation (Wissinger 1989; Suhling and Suhling 2013; Rasmussen et al. 2014). Also, differences in egg development may have the same effect since eggs of some species may develop directly after oviposition while others undergo a diapause mainly to circumvent adverse winter conditions (Corbet 1999; Jingui et al. 2010; Schiel and Buchwald 2015). And, finally, differences in oviposition date may lead as well to strong size differences between larval populations (Fincke 1999; Padeffke and Suhling 2003). In the latter two cases this may be addressed as temporal priority effects for the earlier laid or earlier hatching egg.

We studied two common and widespread European dragonfly species, which co-occur in various mostly lentic habitats, such as ponds and lakes. The sibling dragonfly species *Sympetrum vulgatum* (Linnaeus, 1758) and *S. striolatum* (Charpentier, 1840) are sympatric and syntopic in major parts of Europe (Boudot and Kalkman 2015). However, the two species differ in their population trends in Germany: while the occupancy of *S. striolatum* is increasing, declines of *S. vulgatum* are observed (Bowler et al. 2021). In the first half of the twentieth century, *S. striolatum* was very rare in northeastern Germany, whereas *S. vulgatum* was common in that region (Münchberg 1930). Thus, there may be a long-term and large-scale trend of species turnover, which may be associated with the corresponding climate warming. We aimed to investigate possible mechanisms causing the diverging population trends between these two species. An initial literature overview of 95 publications from most of the range of both species (Supplementary material) revealed that the species are quite similar in morphological and behavioural traits, as well as in habitat selection, and voltinism. However, there are hints that the species may differ in oviposition environment (habitat), overwintering (i.e. in the egg or larval stage), and growth rate:

- The oviposition of *S. vulgatum* is assumed to occur more commonly in shrinking parts of lentic waters (Wildermuth and Martens 2019), so that the eggs may be more prone to drying during the winter season. Oviposition site selection along a terrestrial-aquatic gradient may have consequences for hatching success (Martin and McCauley 2021). Furthermore, the egg development and hatching can be influenced by humidity, photoperiod, temperature, or hypoxia (Corbet 1999). According to our literature overview, the clutches of *S. vulgatum* are laid more frequently at the edge of the waterbodies (Münchberg 1930; König 1990; Rehfeldt 1992). Therefore, the
risk for the eggs of *S. vulgatum* to lay temporarily outside of the water body may be higher, especially during the winter.

- Many species of *Sympetrum* overwinter in the egg stage and according to Schiel and Buchwald (2015) the majority of *S. striolatum* hatches before winter, i.e. overwintered in early larval instars, whereas the majority of *S. vulgatum* hatched in the next spring, hence overwintered in the egg stage, which may cause general differences in winter survival, but would also inflict priority effects between the species (see above).
- Initial data imply that while the general temperature response of growth was similar *S. striolatum* had a higher maximum growth rate (Suhling et al. 2015), which as well could inflict asymmetric size-mediated intraguild predation, and we expected *S. striolatum* growing faster.

We therefore investigated embryonic development under simulated drought vs. water and direct vs. delayed development treatments. We hypothesised that differences in embryonic development may lead to differences in survival until hatching and the hatching process under various environmental conditions. Eggs laid in non-permanent or shrinking waterbodies may suffer of potential drought periods, and this may cause higher losses in *S. vulgatum*. We also aimed in gathering more data on overwintering stage, since this may be critical for intraguild predation. In addition, the larval growth was examined because differences in timing of development may cause a phenological mismatch and ultimately increase size-mediated intraguild predation, and we expected *S. striolatum* growing faster.

### Methods

#### Experimental design

Two experiments were carried out. The first experiment observed the egg development and hatching behaviour under different environmental conditions and the second experiment examined the growth rate of the larvae during the first months. For both experiments we obtained eggs of the *Sympetrum* species by catching copulating or ovipositing pairs. For gathering an egg clutch a female’s abdomen was dipped several times into a tube with water (Robert 1959). All clutches of *S. striolatum* and *S. vulgatum* were collected in two pondscapes 5 East and 20 km north of Braunschweig, Germany in late summer 2020, between the 19th August 2020 until 11th September, 2020. The aim was to keep the sampling period as short as possible to reduce potential seasonal effects during sampling. Three weeks is relatively short compared to the several months flight season of both species. Eleven clutches with a total of 11,492 eggs of *S. vulgatum* and ten clutches with 8,616 eggs of *S. striolatum* were collected for the laboratory experiment (Table S1), which also permits studying intra-species variations. Such an extensive study of these two species has not been done before.

The eggs were directly transferred to the laboratory. All experiments were carried out under the same general laboratory conditions. We used tap water, which was dechlorinated by filling it into containers some days prior to the experiments. Our intention was to simulate a warm late summer in September and for clutches with a delayed development a warm spring, respectively. Therefore, a daylength duration of 14 h was chosen. Illumination was by LED daylight lamps (1600 lx). Temperature in the lab varied from 18–22 °C.

#### Egg development

In our experiment we simulated two possible conditions:

- Varying egg environment: The eggs are laid in deeper water where they remain or at the edge of the pond and may fall dry later in the year
- Varying development: The development begins directly after oviposition or only after a delay, possibly a diapause, due to cold conditions or winter daylengths.

In order to investigate how egg development responds to a potential terrestrial stay and how this affects embryonic development, a drought was simulated by placing eggs on filter paper on absorbent cotton soaked with water. The eggs remained humid as they would on wet soil. Development was compared to eggs placed in water. Between these conditions the factors humidity, temperature and hypoxia may act differently on a clutch.

Since the two species appeared to differ in development (Schiel and Buchwald 2015), we included direct vs. delayed development into our experimental setup. We simulated a delayed development by a 28 days stay in a fridge at 5 °C. This temperature was chosen because in *S. striolatum* no embryogenesis occurred below 6 °C (Koch 2015). In the fridge the light period was also reduced to eight hours to match winter conditions. After the 28 days in the fridge, the eggs were transferred gradually to room temperature. During the change to room temperature also the daylength duration was slowly increased over two weeks with approximately an additional half hour per day from 8 to 14 h. These conditions do not exactly resemble winter in Braunschweig, but similar settings were successfully used in other experiments with *S. vulgatum* to simulate winter conditions even further north (Everling and Johansson 2022).

We divided each egg clutch into four parts for both species so that eggs of each clutch were experiencing the same four treatments (Fig. 1). The numbers of eggs were not
exactly similar since it is sometimes difficult to separate them from each other, but all were counted before starting the experiment (Table S1). The filter paper approaches were named (a) and (c). Treatment (a) was kept for delayed development in the fridge as described above. Approach (c) was kept throughout at room temperature. Due to evaporation the treatments were checked regularly and watered as needed. For the experimental part of clutches in water, the dishes were filled with 50 ml of untreated and stale tap water and the eggs were added. The permanent water approaches were labelled with (b) and (d). Treatment (b) was kept for the delayed development. Treatment (d) was kept in water at room temperature permanently.

The treatments were monitored daily after the first week of experiment. The freshly hatched larvae were counted and removed from their containers to prevent double counting. An exact time series of the hatching events for each of the four treatments and of each clutch was recorded. With these data the development time of the clutch until first hatching, the hatching rates in % of the total number of eggs per treatment and clutch and the hatching curves over time were plotted. To characterize and compare the shape of the hatching curves, the quantiles of 50% (Q50) and 90% (Q90) of the larval hatch were determined from the cumulative function. ANOVA in R was performed to identify differences of the duration of egg development, the hatching duration, the hatching rates and the Q-values. The independent factors were species (S. striolatum vs. S. vulgatum), the development (delayed vs. direct) and the egg environment-treatments (in water vs. on land). Additionally, egg clutch was tested as random factor with the R-package “lme4” (Bates et al. 2015).

Larval growth

For investigating larval growth, we used only larvae of the treatments (b) and (d) because the numbers of surviving larvae on the filter paper in treatments (a) and (c) was low (3.7% of total). The larvae were reared at room temperature (see above) in tap water and fed daily with naupliae of Artemia salina ad libitum. The larval maximum head widths were measured weekly. Only larvae that could be measured at least five times were used to fit a regression for growth over time. For each treatment the linear and exponential regression were fitted to get the mean growth rates over time. Both models have been used before e.g. (Suhling et al. 2004, 2005). The model performance of the two fits was compared using the coefficient of determination $R^2$ for each measured approach. To obtain an as accurate as possible growth rate, the regression method better fitting the data (evaluated by $R^2$) was used (Table S2). ANOVA was performed for analysing the growth in dependence of the species (S. striolatum vs. S. vulgatum), egg environment (filter paper vs. water), and development delay (delayed vs. direct) treatments.
Results

Egg development

The duration of egg development of the two species differed strongly with *S. striolatum* developing much faster and without huge intraspecific differences. In contrast, *S. vulgatum* showed strong variations between the clutches and their egg development took more days compared to *S. striolatum*. Note that the values for the egg development duration of the delayed treatments (a) and (b) in Table 1 include the 28 days of delayed development, i.e. low temperature. If these 28 days are excluded, the average development time for both species corresponded to the results of clutches without diapause (values in parentheses in Table 1). Thus, a diapause during embryonic development primarily seemed to lead to a postponed development process, but did not have much influence on the total required egg development time. Therefore, we used the adjusted values for the treatments (a) and (b) for analysis (Table 2).

The duration of egg development of the two species differed significantly with the eggs of *S. striolatum* developing faster. Intraspecific variation was also obviously lower in *S. striolatum*. The effect of the temperature and the interaction of species x development delay were represented in the changing hatching behaviour of *S. vulgatum*. For *S. vulgatum* the cold break during embryogenesis led to a more synchronised hatching process and decreased the intraspecific variation in egg development duration.

The hatching rates differed between the species, with *S. striolatum* having higher rates than *S. vulgatum* (Table 1). Moreover, the hatching rates were also significantly influenced by the development treatment. The eggs without delayed development had a higher hatching success in both species. Also, the environment affected the hatching rates: eggs kept in water instead of on filter paper hatched in higher numbers and showed a significant effect of the

| Table 1 Egg development and hatching of *S. striolatum* and *S. vulgatum* |
|-----------------------------|-------------------------|-------------------------|-------------------------|------------------------|
| Treatment                   | Egg development duration [d] | Hatching rate [%] | Hatching duration [d] | Q50 [d] | Q90 [d] |
| *Sympetrum striolatum*      |                          |                        |                        |          |          |
| (a)  Delayed/wet           | 40.8 ± 1.2 (12.8 ± 1.2) | 63.9 ± 17.5 | 83.4 ± 24.5 | 2.2 ± 1.0 | 8.1 ± 4.4 |
| (b)  Delayed/dry           | 43.0 ± 1.3 (15.0 ± 1.3) | 41.6 ± 17.9 | 97.7 ± 19.8 | 17.9 ± 6.8 | 28.7 ± 8.9 |
| (c)  Direct/wet            | 11.4 ± 0.7 | 64.7 ± 19.0 | 59.5 ± 50.5 | 1.2 ± 1.2 | 7.8 ± 8.1 |
| (d)  Direct/dry            | 12.5 ± 1.0 | 59.5 ± 15.1 | 72.4 ± 27.0 | 4.9 ± 3.3 | 26.2 ± 12.1 |
| *Sympetrum vulgatum*       |                          |                        |                        |          |          |
| (a)  Delayed/wet           | 45.5 ± 6.0 (17.5 ± 6.0) | 46.5 ± 10.8 | 157.0 ± 20.1 | 48.4 ± 13.1 | 77.5 ± 13.4 |
| (b)  Delayed/dry           | 48.8 ± 11.3 (20.8 ± 11.3) | 21.2 ± 18.1 | 151.1 ± 18.6 | 40.5 ± 29.2 | 81.6 ± 21.0 |
| (c)  Direct/wet            | 26.5 ± 14.7 | 62.7 ± 14.6 | 150.9 ± 21.5 | 51.0 ± 15.6 | 90.4 ± 16.8 |
| (d)  Direct/dry            | 31.7 ± 14.3 | 28.2 ± 20.4 | 135.1 ± 17.3 | 39.5 ± 14.0 | 74.5 ± 17.1 |

All values are means per clutch ± S.D. Egg development duration: numbers of days per egg clutch from egg deposition until first hatch (in parentheses: 28 days delayed development substracted). Hatching duration: numbers of days form first until last hatching. Hatching rates: % of the total number of eggs per treatment and clutch. Q50: quantiles of 50% and Q90: quantiles of 90% of the larval hatch determined from the cumulative hatching curves.
oviposition treatment and the interaction of species x environment (Table 2). This effect was more pronounced in *S. vulgatum*, where only about 20% hatched in dry conditions. The larval endurance after hatching differed notably between the egg environment treatments: survival on filter paper was 4.3% in *S. striolatum* and 3.1% in *S. vulgatum*, while the numbers in water were 93.7% and 91.6%, respectively.

The cumulative hatching curves differed between species (Fig. 2). In *S. striolatum* the hatching was more synchronised over all egg clutches than in *S. vulgatum*. In fact, the complete hatching process of *S. vulgatum* took in some cases twice as long as in *S. striolatum*. All hatching curves of *S. striolatum* displayed a very similar and concentrated distribution. Especially the Q50, but also the Q90 were reached within a short period after hatching started (Table 1 and Fig. 2). This pattern was apparent both for the experimental approaches within a clutch and for all clutches in comparison. The hatching curves of *S. vulgatum* were considerably less synchronised and larvae hatched for months.

**Fig. 2** Hatching curves of *Sympetrum striolatum* and *S. vulgatum* in the different conditions. Dashed: Q50 (0.5) and Q90 (0.9); black: development direct (treatments c, d); grey: development delayed (treatments a, b). For convenience, the individual clutches are not marked separately.
striolatum. Consequently, Q\textsubscript{50} and Q\textsubscript{90} were significantly different between the species. Also, the species x environment interaction term differed significantly. For S. striolatum the treatments in water reached the Q\textsubscript{50} and Q\textsubscript{90} faster than their eggs kept on filter paper. This interaction was only reflected in the data of S. striolatum and therefore an influence of the egg environment could be assumed at least for this species. There was also a significant effect of the random factor clutch on development duration, hatching rate and hatching curve, which is mainly reflected in the high variations recorded in S. vulgatum.

Larval growth

The larvae of S. vulgatum grew significantly faster than those of S. striolatum (F\textsubscript{1,33} = 35.217, p < 0.001). The mean growth rates per day differed by slightly more than 0.01 mm per day between the two species, regardless of whether the eggs were from the delay treatments or not (Fig. 3). The effect of delay vs. direct development was as well significant (F\textsubscript{1,33} = 4.392, p = 0.0439), while the interaction was not significant (F\textsubscript{1,33} = 0.006, p = 0.939).

Discussion

Our study revealed three major disparities that may explain different population trends of S. striolatum and S. vulgatum. Hatching rates were reduced under simulated drought conditions, and particularly so in S. vulgatum. While the eggs of S. striolatum developed rapidly and hatched highly synchronously, the development of S. vulgatum varied widely between clutches and most eggs hatched much later than those of S. striolatum, independently of experiencing a simulated winter diapause or not. And finally, larvae of S. vulgatum grew significantly faster under simulated autumn and spring conditions, i.e. when main development of young instar larvae may occur.

The egg deposition site may have a significant effect on egg survival (Brock et al. 2013; Martin and McCauley 2021). Depending on where the eggs are located during oviposition, environmental factors like hypoxia, temperature, or predation influence egg mortality and hatching of different Sympetrum species (Jinguji et al. 2010; Martin and McCauley 2021). The clutches of both our species can develop on land or moist soil. However, the development of the clutches outside the water seems to have a negative effect on the hatching rate of both species. As S. vulgatum lays more frequently at the water’s edge the risk for clutches of this species to lie outside the water is probably higher since autumn rainfalls in most of Central Europe are usually lower than summer rainfalls (DWD 2020) and may not re-fill the ponds. In our experiments hatching rate of S. vulgatum in dry condition was reduced by more than half compared to development in water, while the losses of S. striolatum were lower. Thus, our data imply a disadvantage when ponds dry during summer and may not be sufficiently re-filled in spring due to increasing aridity. In England S. striolatum is typical for such ponds (Corbet 1956). However, the hatching rates observed by Schiel and Buchwald (2015) in more southern populations were reversed and more in favour of S. vulgatum (but with lower numbers of eggs reared). Thus, we cannot exclude that local population factors play a role, i.e. southern S. vulgatum eggs had better drought survival. It also remains to be investigated whether there are morphological differences between the eggs of both species, such as the thick and impermeable vitelline envelope in the eggs of S. sanguineum increasing resistance to freezing and drying (Sahlein 1994). Whatsoever, also in our experiments S. striolatum did only survive drought better as long as the egg development lasted. Hatching was fatal in both species under dry conditions. At the time of hatching, survival requires water coverage or
eggs need to lie directly at the water’s edge so that the larvae reach the water. In addition, it needs to be recognised that S. striolatum has a second strategy to cope with drying: in the Mediterranean, where most habitats dry out in summer, the adults emerge early in the season and postpone maturation until autumn (Samraoui et al. 1998). Such a pattern may also arise in Central Europe with ongoing climate change.

We found striking differences in embryonic development, which may affect the interactions between the larvae of both species subsequently. This refers particularly to the synchronisation of hatching. Eggs of S. striolatum developed rapidly and hatched highly synchronously without any strong intraspecific variation. We found no increase in synchronisation due to a cold period as observed by Koch (2015). Also, data by Schiel and Buchwald (2015) imply somewhat longer hatching periods than observed by us. This could be due to egg-laying time and more southern location. Hatching speed of other Sympetrum species is affected of photoperiod and temperature (Jinguji et al. 2010). As all clutches for our study were collected during a narrow time window of the long oviposition period of S. striolatum, possible seasonal effects remained unregistered. Sympetrum vulgatum hatched much less synchronised, although in this species we found a synchronising effect of initial cold. Occasionally, larvae may hatch in the year of egg laying, depending on egg-laying time and temperature (Münchberg 1930; Schiel and Buchwald 2015). But according to Münchberg (1930) larvae hatching in the same year died, which led to the assumption that only in the case of eggs laid early, development seems conceivable in the same year. This demonstrates a certain variability, which will be discussed below.

Besides all possible exceptions, we may assume that under most circumstances most S. vulgatum would hatch much later than the vast majority of S. striolatum. This concurs with earlier observations implying that an egg diapause is typical in S. vulgatum and rather uncommon in S. striolatum (Münchberg 1930; Corbet 1956; Robert 1959; Schiel and Buchwald 2015). While overwintering in the egg is normally perceived as an advantage (discussion in Martin and McCauley 2021) our data imply also a possible disadvantage: In our experiments hatching rates decreased significantly after the delayed development. Hence, a delayed development would have a negative effect on the hatching success of a clutch as mortality rises.

One can assume that, as a result of faster egg development, normally larvae of S. striolatum are present in the habitat several months before S. vulgatum, depending on the time of oviposition, which may start in July and end in November Wildermuth and Martens (2019). Due to low temperatures the larvae spend more time in early instars until about April or May before increasing temperature speeds up development (Corbet 1956). Some few larvae of S. vulgatum may also overwinter in early instars but the vast majority may only hatch in the following spring (Schiel and Buchwald 2015). Thus, there is a case of temporal advantage (i.e. temporal priority), causing larvae of S. striolatum being about in the fourth instar (Corbet 1956) when S. vulgatum larvae hatch. In Odonata such size differences often trigger size-dependent intraguild predation (SDIP) (Suhling and Suhling 2013; Rasmussen et al. 2014). Predation within the guild can be responsible for an estimated 25–45% of total larval mortality in autumn (Wissinger 1989). As both species inhabit the same water bodies and the larvae of both species prefer the shallow and warm shore areas, we presume strong asymmetric SDIP by S. striolatum on S. vulgatum. With S. striolatum increasing its population size north-eastwards also the mortality of S. vulgatum may rise in regions where S. striolatum did not previously occur.

At ambient temperature of ca 18–22 °C larvae of S. vulgatum grew 0.01 mm per day faster than S. striolatum. Temperature response experiments confirmed a steeper curve of S. striolatum, i.e. S. striolatum growth more rapid at higher but slower at lower temperature (Suhling et al. 2015). The more rapid growth of S. vulgatum especially in cooler waters could gain into a size advantage over S. striolatum, when the larvae of S. vulgatum hatch early enough before those of S. striolatum. Hence, the growth advantage of S. vulgatum may equalise to some extent the temporal advantage of S. striolatum. The net effects need to be experimentally evaluated. The rapidly growing Sympetrum fonscolombii cannot catch up a 11 days advantage of the slower growing Trithemis kirbyi (Padeffke and Suhling 2003). However, due to the risk-spreading behaviour of S. vulgatum (see below), only few larvae will be able to benefit from such advantage.

Other factors may be also in favour of S. vulgatum. Early instar larvae of S. striolatum were unable to survive water temperatures below 4 °C at laboratory conditions (Koch 2015). Even if the conditions may differ a bit in natural habitats one may conclude that longer periods of very cold temperature may have adverse effects on larvae of S. striolatum. Also, a habitat suitability model emphasizes that 4 °C may be a winter minimum for this species (Koch et al. 2012). Thus, in cold winters, survival of S. striolatum larvae may be reduced and only those eggs that diapause during winter may produce offspring. In such case there would be no temporal advantage. Moreover, the spread-out hatching period of S. vulgatum may be interpreted as risk spreading (Koch and Suhling 2005; Martin and McCauley 2021). While autumn hatching larvae may stand a chance in SDIP due to their higher growth rates (see above), spring-hatching eggs probably suffer less mortality in winter, i.e. some survival would be possible under different conditions. Temporal risk-spreading may be an important factor for both species as both have a long flight and egg-laying period. Due to the long-lasting oviposition period of S. striolatum and S.
**Conclusions**

We assume four possible scenarios for the interaction dynamics of the two species in central Europe:

**Scenario 1**

Sympetrum striolatum hatches in autumn of the year of oviposition. Most clutches of S. vulgatum spend the winter in diapause and the larvae hatch in the following spring. The considered water body is a permanent water body during a mild winter. The larvae of S. striolatum survive the winter in large numbers causing a clear size advantage and consequently a strong asymmetric intra-guild predation on small S. vulgatum. In summer, S. striolatum would be more numerous than S. vulgatum.

**Scenario 2**

Sympetrum striolatum hatches again in autumn of the year of oviposition and most of the eggs of S. vulgatum spend the winter in diapause. The population of S. striolatum gets substantially reduced during cold winter and while S. vulgatum hatch in spring and survive in large numbers. This pattern would support the assumption of Wildermuth and Martens (2019) that after cold winters the number of S. striolatum decreases significantly compared to S. vulgatum.

**Scenario 3**

Most larvae of both S. striolatum and S. vulgatum hatch in autumn of the year of oviposition. Although S. vulgatum grows slightly faster, the egg development of S. striolatum is much shorter. Hence, their larvae have a large developmental advantage over the larvae of S. vulgatum, which probably would cause many larvae of S. vulgatum being prey for S. striolatum, resulting in an increased occurrence of S. striolatum in the following year.

**Scenario 4**

The clutches of both species spend the winter in diapause. The larvae of both species hatch in spring. However, as in the first scenario, S. striolatum has still the advantage of the rapid embryonic development.

Of course, it must be kept in mind that the results of this study only give hints about the processes under natural conditions. Neither all eggs are laid at the same time nor all larvae of a population will hatch at the same time. Due to the flexible life cycle models, different larval stages of both species will colonise the same habitats in time and space. Surely other factors and variables play into the population development processes that are not yet finally understood and described. However, our data provide some explanation for the diverging population trends of these two common species. While S. vulgatum had an advantage in cooler waters and in cold winters S. striolatum would strongly benefit from recent warming and drying and will potentially dominate over S. vulgatum also further north in Europe.

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