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Research article

A broader flight season for Norway's Odonata across a century and a half

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As global climate continues to change, so too will phenology of a wide range of insects. Changes in flight season usually are characterised as shifts to earlier dates or means, with attention less often paid to flight season breadth or whether seasons are now skewed. We amassed flight season data for the insect order Odonata, the dragonflies and damselflies, for Norway over the past century-and-a-half to examine the form of flight season change. By means of Bayesian analyses that incorporated uncertainty relative to annual variability in survey effort, we estimated shifts in flight season mean, breadth, and skew. We focussed on flight season breadth, positing that it will track documented growing season expansion. A specific mechanism explored was shifts in voltinism, the number of generations per year, which tends to increase with warming. We found strong evidence for an increase in flight season breadth but much less for a shift in mean, with any shift of the latter tending toward a later mean. Skew has become rightward for suborder Zygoptera, the damselflies, but not for Anisoptera, the dragonflies, or for the Odonata as a whole. We found weak support for voltinism as a predictor of broader flight season; instead, voltinism acted interactively with use of human-modified habitats, including decrease in shading (e.g. from timber extraction). Other potential mechanisms that link warming with broadening of flight season include protracted emergence and cohort splitting, both of which have been documented in the Odonata. It is likely that warming-induced broadening of flight seasons of these widespread insect predators will have wide-ranging consequences for freshwater ecosystems.

Keywords: anthropogenic disturbance, Bayesian models, flight season, gamma regression, phenology, voltinism

Introduction

Anthropogenic disturbance, direct or indirect, has already disrupted and is expected to further disrupt many ecosystem processes, often through depletion or alteration of insect communities. In wetlands, for example, changes in maximum ambient temperature, precipitation seasonality, and evaporation rates, which affect ephemerality of water, are expected to reshape invertebrate assemblages (Epele et al. 2022).



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Mechanisms that reshape assemblages will vary (Traill et al. 2010), but species-specific changes in phenology are expected to be common (Woods et al. 2022).

Phenological shifts have received considerable attention since at least the mid-1990s. Emphasis has been placed on shifts at the front end of the activity window, such as earlier blooming or earlier emergence (Parmesan 2007, Cohen et al. 2018, Hill et al. 2021, Zettlemoyer and DeMarche 2022), being framed typically, for volant insects, as an expectation of an earlier leading edge or the mean date of the flight season (Duchenne et al. 2020, Gutiérrez and Wilson 2021). This emphasis may lead to publication bias: a meta-analysis of marine organisms found that phenology tended to be measured in spring and summer but only 'rarely' in autumn or winter (Brown et al. 2016). As such, autumn has been called the 'neglected season' with respect to studies of ecological response to climate change (Gallinat et al. 2015).

A lack of attention to autumnal responses has potentially profound ramifications on our understanding of how phenology shifts across species. Warmer autumns are on the increase in the Northern Hemisphere (Liu et al. 2016), with particularly sharp relative increases in ambient temperature in September, October and November (Renner and Zohner 2018). Extreme warming in the latter half of a year opens the possibilities both that flight season will lengthen and that the trailing edge of the season will extend to the point of either pulling the mean rearward or skewing the distribution rightward. There is evidence that flight season may lengthen, as reported in, for example, migratory aphids (Hemiptera: Sternorrhyncha) in England (Bell et al. 2015) and butterflies (Lepidoptera) in Massachusetts (Michielini et al. 2021), but the phenomena of lengthening (increased variance) and increased skew are little studied. An increase in phenological breadth without a change in central tendency may affect ecological systems on individual and population levels (Zettlemoyer and DeMarche 2022). Furthermore, knowledge of the whole phenological distribution and not solely a single metric such as a point estimate of the mean or leading edge is necessary to assess temporal overlap among species properly (Carter et al. 2018), which in turn allows for proper inference about ecological effects.

We analysed how flight season of the insect order Odonata, the dragonflies and damselflies, has changed across the past century-and-a-half in Norway. Odonate species emerge from freshwater habitats (excepting a handful of Australasian species whose nymphs develop on land) during warm months, and adults fly solely during warm months. Longevity ranges from several months to several years as aquatic nymphs but from only a few days to as many as a few months as adults (Paulson 2019). It is unclear which stage, nymph or adult, is most limiting to population growth and stability, yet all reproductive activity, from territoriality to mating to oviposition, takes place in that short time when adults are volant. Warmer temperatures could advance or extend flight season, with potentially profound consequences for ecosystems given that all odonate species, regardless of life stage, are both important predators and prey in the middle tiers of

freshwater food webs (Bried et al. 2020, Sentis et al. 2023). Interspecific variation is expected, variation that is predicted to disrupt ecological interactions (Carter et al. 2018, Renner and Zohner 2018, Duchenne et al. 2020, Iler et al. 2021). Yet, it remains unclear which species will respond to climate change by, say, broadening a flight season – a process (sensu Inouye et al. 2019) with potentially many ecological ramifications – and which species, for whatever reasons, will be unable to respond. There is growing evidence, albeit not without confutation, that intrinsic voltinism and its plasticity will prove to be a key explanatory factor for shifts in insect activity patterns.

Voltinism, the number of generations per year, varies across the Odonata (Corbet et al. 2006), with species or populations variously being multivoltine (≥ 3 generations/year), bivoltine (two generations/year), univoltine (one generation/year), semivoltine (one generation/two year), or partivoltine (one generation/three + years). Voltinism decreases monotonically with increasing latitude (Corbet et al. 2006, Zuess et al. 2017, Grevstad et al. 2022) but does not vary strictly with body size (Teder 2020). It is, however, associated with warmth. Many insects hatch more quickly and develop to adulthood more quickly when exposed to warmer conditions (Stoks et al. 2014, Frances et al. 2017, McCauley et al. 2018, Pollard et al. 2020), suggesting the potential for quickened life histories with climate change, especially because thermal accumulation (degree-days) in a growing season appears to be the principal driver of phenology of hatching, development, and emergence (Cayton et al. 2015, Grevstad et al. 2022, Woods and McGarvey 2023). As growing season lengthens (Reyes-Fox et al. 2014), shifts toward shorter generation time imply potential for more generations per year and, hence, potentially longer flight seasons. The same may hold for land-use changes that reduce canopy cover (with an attendant increase in radiative warming), as in a report of a 'sudden' switch from partivoltine to semivoltine in a population of *Aeshna cyanea* for which logging exposed to direct sunlight a formerly shaded breeding site in southern Sweden (Norling 2021). Additional temperature-mediated scenarios also could alter voltinism or other life history traits. Warm-adapted species (i.e. including all odonates) may as a rule expand their flight season rather than advancing the mean.

Our focus was on the form of phenological response in odonates, not on climate change itself, for which there is an abundance of evidence: Scandinavia already has warmed and is forecast to become both warmer and wetter in coming decades (Christensen et al. 2019), and growing season there has lengthened markedly (Linderholm 2006). We specifically assessed the extent to which odonate species shifted mean flight date versus broadened their flight season – a contrast between a shift in mean versus a shift in variance – and we assessed the extent to which flight season has become more skewed. We did so by estimating, from a vast citizen science database, the mean, variance, and skew of each flight season from 1845 to 2021, after which we analysed the extent to which the mean, variance, or skew has shifted over that 170 year window. For all models we took into account uncertainty

associated with sampling effort, which, not surprisingly, has varied considerably from the earliest records to the most recent records (i.e. a sharp increase in data beginning in 1990 and especially after 2005). When we found a shift in phenology, we explored the extent to which a voltinism hypothesis (as well as factors that affect voltinism, such as shading or oviposition site) could account for it.

Material and methods

Dataset

Occurrence data for flight seasons of Norway Odonata were obtained from Artsdatabanken (www.artsdatabanken.no/), a publicly available citizen science database. We excluded any record not identified to species or that pertained to a nymph, lacked a specific date of record, or was a sight record on a date notably outside the known Scandinavian flight period (Billqvist 2019), and we filtered the dataset to remove duplicate entries. We flagged as valid any records that mentioned adult activities (e.g. reproduction, flying, courtship, mate guarding) or any labelled as male or female (nymphs cannot be sexed, so sexed individuals must be adults). Between 4000 and 5000 records not otherwise flagged were supported by photographic documentation; we examined every photo to exclude nymph-only records. For the remaining records, a colleague familiar with the dataset (Kjell Magne Olsen, in litt.) named persons known to work on nymphs so we could exclude those particular records and confirmed that records submitted via Biofokus (<https://biofokus.no/>) would be of adults. After cleaning, we reduced the nearly 56 000 records to just over 35 000 records. We pooled data across the country. Norway spans many latitudes, but then and now most records are for the southern fifth of the country, so there is no relationship between year and latitude (Kendall's $\tau = -0.01$) that could confound analyses.

Species attributes

We selected predictors that bore directly on hypotheses related to generation time, including those reasonably associated with warming. They were 1) voltinism, 2) number of anthropogenic habitats used (seven categories [aquaculture ponds, salt exploitation, excavations, wastewater facilities, irrigated land, seasonally flooded agriculture and canals/ditches] of 20 possible; this predictor and the next could relate to voltinism indirectly via exposure to direct sunlight), 3) % shade at occupied sites, 4) oviposition site (endophytic or exophytic; related to voltinism via hatching time) and 5) overwinter stage (egg or nymph; affects voltinism directly). Data on habitat use and life history were obtained from www.dragonfly-database.eu (Harabiš and Hronková, 2020), gaps in which we filled with data gleaned from other papers (Adamović et al. 1996, Johansson and Brodin 2003, Rychła et al. 2011). Voltinism was reported in that database, but we opted to obtain a weighted average across studies summarized by Corbet et al. (2006), who scored

voltinism as: multivoltine, three; bivoltine, two; univoltine, one; semivoltine, 0.5; and partivoltine, 0.3. Hence, ours was an estimate for a given species of the average number of generations per year. We classified a Harabiš and Hronková (2020) habitat category as anthropogenic if it was both manmade and disturbed routinely. A reservoir is manmade but often supports abundant natural vegetation in which a more-or-less natural ecosystem may thrive. By contrast, a gravel pit that sporadically retains water is both manmade and disturbed. Of the 42 species initially under consideration, we had to exclude two (*Coenagrion armatum* and *C. johanssoni*) from subsequent analysis because sufficient attribute data were lacking.

Statistical analyses

As a general assessment of how mean, variance, and skew have changed annually, we plotted, across all Odonata, shifts in mean (earlier or later), breadth (broader or narrower), and skewness (right or left) to assess evidence of 'runs', a series of like directional shifts, such as broader variance or right skew. The logic was to ensure we mapped only those means, variances, or skews that definitely differed from the long-term average (for the mean and standard deviation, the square root of the variance) or from zero (for the skew) to account for uncertainty by not mapping values that could not reasonably be distinguished from the null. We defined 'definitely' as an estimate outside the 95% highest density intervals ('HDI' R package (www.r-project.org) 'HDInterval', Meredith and Kruschke 2020). The end result was a series of data that could be thought of as 'present' (evidence for a shift), 'absent' (no evidence for a shift), or 'NA' (insufficient data to estimate moment). To these data we adapted, in R (www.r-project.org), a Bayesian 'hot hand' test (Wetzels et al. 2016) to obtain Bayes factors (Kass and Raftery 1995) that weighed support for a run against a null of random toggling back and forth. We ran the test in two ways: 1) only years with definite shifts in a moment were included or 2) years in which a moment could not be distinguished from the null were replaced with a Bernoulli draw with $p = 0.5$, a random 0 or 1. Long-standing categories for evidence against H_0 (Kass and Raftery 1995) are that a Bayes factor < 3.2 indicates there is little to no support for H_A , the model in question, whereas a factor of 3.2–10 indicates 'substantial', 10–100 'strong', and > 100 'decisive' evidence against H_0 . (Bayes factors < 1 provide evidence for H_0 against H_A and can be interpreted in the same categories as 1/BF.)

We estimated the first three moments of annual flight season (ordinal day) for each species or taxon (i.e. order, suborder or family). Estimates were obtained via custom JAGS code, which was run via R package 'rjags' (www.r-project.org, Plummer 2019). Year (x_i) was centred for all analyses to ensure a stable estimate of the intercept. Priors for the mean, μ , were bounded by the calendar year, and priors for the standard deviation, σ , were set to a half-Cauchy (Gelman 2006). These parameters were used to estimate skew, γ , using the standard Fisher–Pearson formulation (Doane and Seward 2011):

$y_i \sim N(\mu, 1/\sigma^2)$	Response variable y distributed normal, with tolerance $1/\sigma^2$
$\mu \sim N(180, 0.001)$ [1,365]	Prior of mean μ normal, bounded by ordinal day extremes
$\sigma \sim \text{Cauchy}(10, 1/2.5^2)$ [0,]	Prior of standard deviation σ half-Cauchy
$SC_i \leftarrow \left(\frac{y_i - \mu}{\sigma} \right)^3$	Sums of cubed deviation (intermediate step for skewness)
$\gamma \leftarrow \frac{n}{(n-1)(n-2)} \sum_i SC_i$	Fisher–Pearson skew, γ

We modelled change in flight season mean and breadth (SD) as a Bayesian gamma regression, generally following the ‘model 1A’ of [Corrales-Bossio and Cepeda-Cuervo \(2019\)](#). This approach was adopted because a standard deviation, the response variable in this study, is distributed χ^2 , which itself is a special case of Γ , and the mean was bounded (i.e. ≥ 0). Also, this step was not strictly hierarchical because uncertainty of estimates of the moments would be driven, in part, by dispersion of individual datum: five records within a few days of each other would have low uncertainty of estimate whereas five records scattered across several months would have high uncertainty. For our purposes, though, uncertainty logically ought to be higher if sample size was smaller. Hence, in our model uncertainty varied with year, and because we had no estimate of survey effort per se, we consider uncertainty $\propto n_i$, the number of records in the i th year. Specifically, we set the upper limit for the prior of the dispersion, φ , to n_i . (Note that the probability density for this formulation of the Γ distribution uses a Γ function with a term in the denominator of, in our case and for integers > 0 , $(\varphi - 1)!$, such that the denominator grows larger with larger n , meaning uncertainty is markedly smaller with larger n .) We thus obtain, for a Γ distribution, parameters of shape φ and rate $\varphi/(\text{the fit line})$:

$y_i \sim \Gamma(\varphi_i, \varphi/\mu_i)$	Response variable y distributed gamma
$\varphi_i \sim U(1, n_i)$	Prior of dispersion φ uniform
$\mu_i \leftarrow \beta_0 + \beta_1 x_i$	Formulation of mean linear
$\beta_0 \sim \text{Cauchy}(10, 1/2.5^2)$ [0,]	Prior of intercept β_0 half-Cauchy
$\beta_1 \sim N(0, 1/\sigma^2)$	Prior of intercept β_1 normal
$\sigma \sim U(0.01, 100)$	Prior of standard deviation σ uniform

This approach had a further impetus and advantage: n_i varied considerably over the dataset, with a sharp increase in records in the past three decades. Parameters from a year with low certainty yield a broad range of estimates, which will tend to flatten regression lines. As for those lines, a positive slope indicated a shift to a later or a broader flight season over the past century and a half (1845–2021), whereas a negative slope indicated a shift to an earlier or a narrower flight season. Skew is centered at 0, so we used a Bayesian analogue of an ordinary least squares regression for it, which amounted to the same model formulation as above except that the response variable was distributed as $N(0, n_i/100)$. Here, a positive slope indicated right skew, a negative slope left skew.

We analysed all data from 1845–2021 because timing of heat anomalies may date to the Industrial Revolution (which ended in ca 1840), as suggested by subsurface temperature data, analysis of which points to measurable warming beginning ca 1800, well before extant meteorological data ([Beltrami et al. 1997](#)). It nevertheless could be argued that warming sufficient to affect volant insects began later than the mid-nineteenth century, so we repeated analyses outlined above with data from 1950–2021, although for these analyses we employed a hierarchical design to set priors for flight season mean and flight season variance on the basis of estimates of those parameters from 1845–1949. For all Bayesian analyses, priors were weakly informative (as described above), three MCMC chains were run with a burn-in of 10 000 iterations and total iterations of 100 000 thinned at 10. We examined MCMC traces of all models to ensure adequate searching of parameter space and checked plots of posterior probability densities to ensure reasonable estimates of parameters.

Resultant slopes from these regressions, one for each species, were used as response variables in subsequent analyses in which we used Bayes factors ([Kass and Raftery 1995](#)) to assess

how well a resultant model provided support for or against H_0 (e.g. an intercept-only model). Our goal was to estimate predictive ability of each attribute on shifts in flight season, with a focus on flight season breadth. Predictors were voltinism, number of anthropogenic habitats, % shade, oviposition site, and overwinter stage (the ‘species attributes’ section for descriptions). Some predictors may act in concert with others; accordingly, we incorporated interactions between 1) anthropogenic habitat \times shade (modification frequently means fewer trees), 2) shade \times voltinism (exposed sites are warmer, hastening hatch and growth rates), 3) the previous two combined and 4) anthropogenic habitat \times oviposition site (modified sites often have reduced aquatic vegetation). We accounted for uncertainty in estimated slopes (β_1), which may vary widely given sample size and intrinsic variance, by use of the ‘probability of direction’ (pd) statistic for each β_1 , the pd being the proportion of the posterior probability density with the same sign as the posterior’s median (Makowski et al. 2019). Hence, the ‘slope’ (pd) can vary from 0 (strongly negative) to 1 (strongly positive), with pd near 0.5 indicating β_1 near 0. Estimates were obtained via the *generalTest* function in R package ‘BayesFactor’ (www.r-project.org, Morey and Rouder 2018) for both additive and interactive models. A single global model fed into this function will produce a list of Bayes factors for all possible model combinations.

Results

We amassed sufficient data to estimate moments for 42 species, of 51 recorded in Norway. There is a strong trend toward broader flight seasons in recent years, particularly since 2000 (Fig. 1). Evidence in support was ‘decisive’:

estimated Bayes factors (BF) were 2449.5 (i.e. $> 2400\times$ greater support for H_A relative to H_0) if only years with definite shifts were included or 514.1 [375.9, 706.8] with ‘0’ years replaced with Bernoulli trials. Support for shifts in flight season mean or skew was weak: for the mean, estimated BF = 3.5 if only years with definite shifts were included or 2.6 [2.2, 3.1] with ‘0’ years replaced with Bernoulli trials, whereas for skew estimated BF = 1.5 if only years with definite shifts were included or 2.5 [2.1, 3.1] with 0 years replaced with Bernoulli trials.

We found strong support for a hypothesis that Odonata flight season has lengthened (Fig. 2A), but our findings contradicted a hypothesis of advanced mean flight season because over time mean flight season is later, not earlier (Fig. 2B). At a finer taxonomic level, flight seasons of the two suborders (Zygoptera, the damselflies, and Anisoptera, the dragonflies), of most families, and of many species have broadened (i.e. variance has increased), but across species shifts in mean were less frequent and were more likely to be delayed than advanced (Fig. 3). Flight seasons of Zygoptera and family Coenagrionidae have become right skewed, but otherwise skew has changed little across species (Fig. 3). Even for species in which a shift in skew was not apparent, there was a signal of a static front edge to the flight season but a delay at the trailing edge (Fig. 4). Considering data only from 1950–2021 did not alter general patterns. For the Odonata as a whole (Supporting information), slopes were highly correlated between the longer and shorter time frames for shifts in mean ($r_s = 0.83$), breadth ($r_s = 0.86$), and skew ($r_s = 0.69$), and general trends held across suborder, families, and species with the strongest signals (Supporting information). For all models, standard diagnostics showed good mixing and unimodal posteriors (Supporting information).

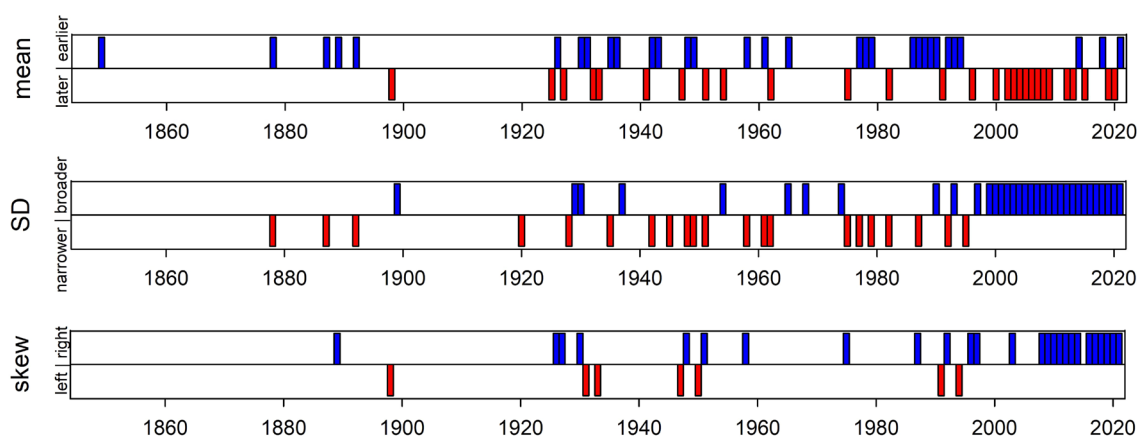


Figure 1. Annual estimates as ‘runs’ (for an associated test) of the first three moments of the flight season of Odonata in Norway, plotted as below (earlier) or above (later) the long-term mean (i.e. an estimate whose 95% credible intervals do not include the grand mean), broader or narrower than the long-term mean for the standard deviation, or above or below 0 for the skew. Years for which an estimate’s credible intervals encompassed the grand mean do not contribute to the analysis – for those years, uncertainty was judged to be too high to map a shift. Note the strong trend toward broader flight seasons since the turn of the millennium and the tendency toward later mean flight season and right skew since then.

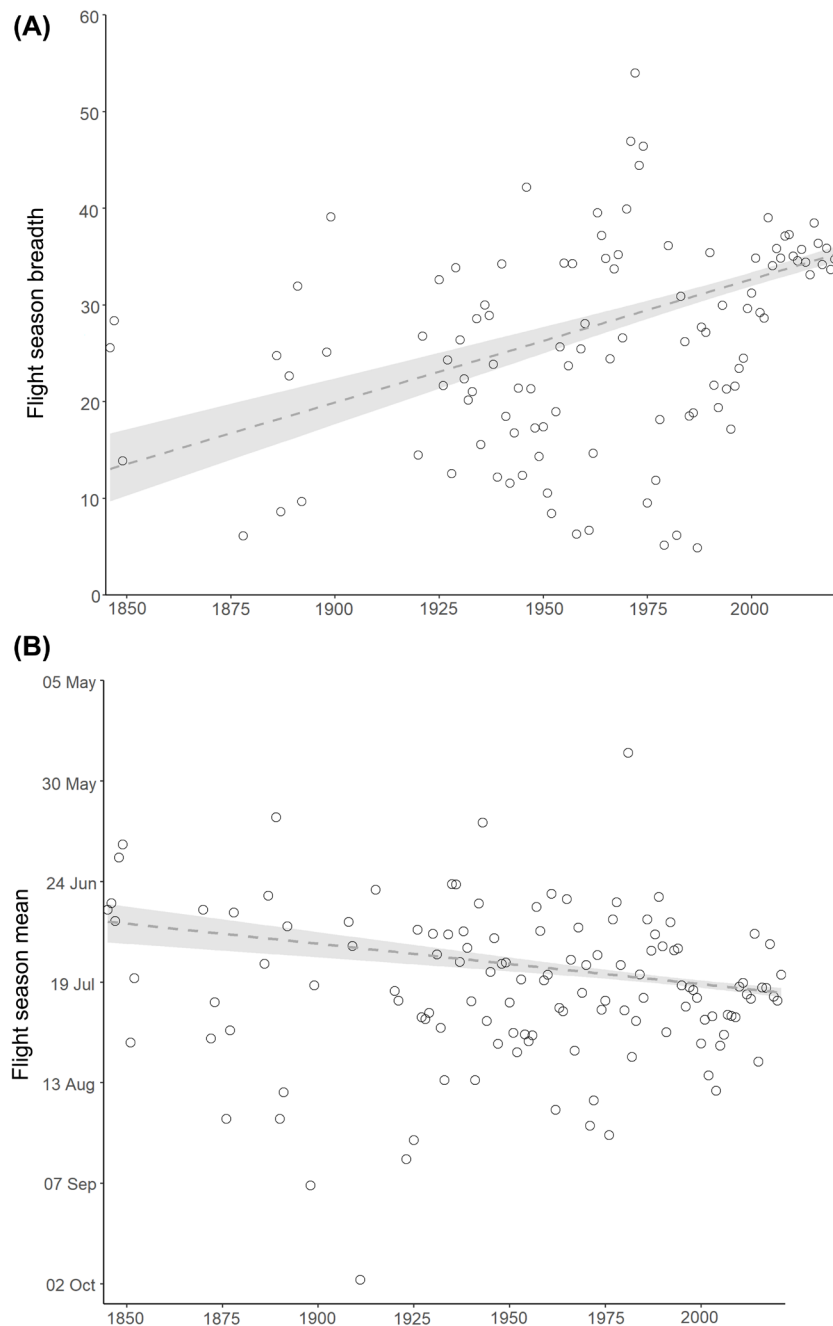


Figure 2. Flight season (A) breadth and (B) mean across 42 species of Odonata (dragonflies and damselflies) in Norway, 1845–2021. Lines are fitted with Bayesian gamma regression and show 95% credible intervals with uncertainty per year adjusted by sampling effort that year (hence, wider CIs in early years).

By itself voltinism was not a strong predictor of flight season breadth (Bayes factor=0.34; i.e., ‘little to no support’, in this case in favour of H_0). The best additive model that included voltinism was likewise weak: voltinism + shade (BF=0.69). By contrast, three complex models that included voltinism as an additive factor provided ‘substantial’ evidence against H_0 . The basic form of the model (BF=3.76) included the number of anthropogenic habitats (related positively, +, to breadth), voltinism (+), and % shade (–) as additive factors

and anthropogenic \times voltinism, anthropogenic \times shade, shade \times voltinism, and anthropogenic \times shade \times voltinism as interaction terms. A model with a somewhat higher Bayes factor (5.90) included oviposition site (–) as an additive factor and shade \times oviposition and anthropogenic \times shade \times oviposition as interaction terms. A model of similar strength (BF=4.24) was identical but included also an oviposition \times voltinism interaction. On the basis of parsimony, it can be concluded that some combination of anthropogenic habitat,

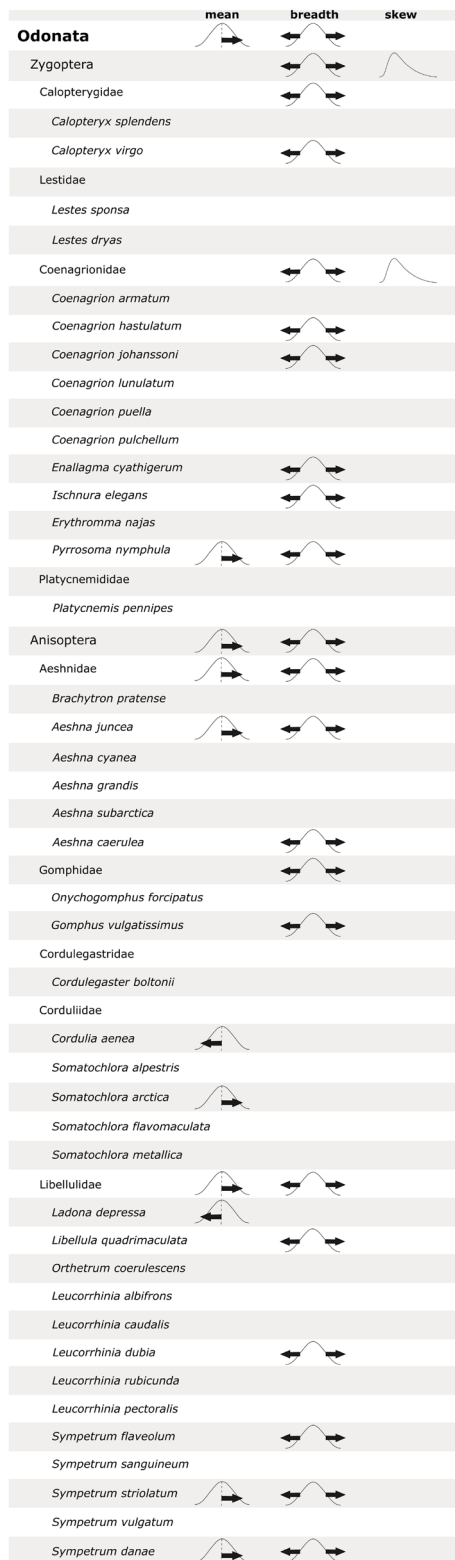


Figure 3. Changes in flight season, as represented by the first three moments of the data distribution, across dragonflies and damselflies in Norway 1845–2021. Arrows show direction of mean shift or change in breadth. In the final column, an asymmetrical shape indicates whether the flight season has skewed right (i.e. sloped to the right) or left over time.

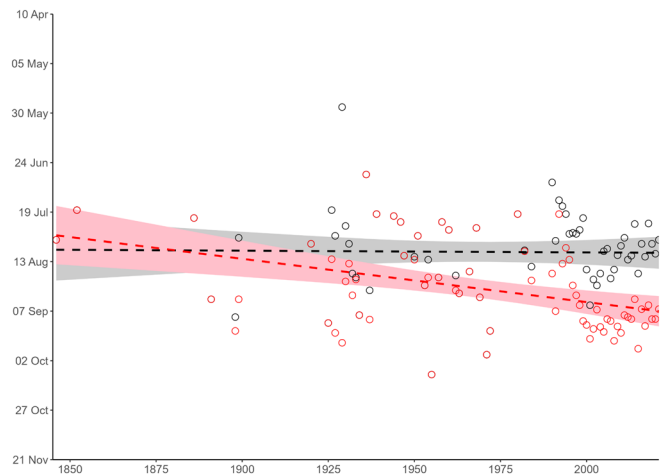


Figure 4. An example of seasonal shifts in flight season, this of *Sympetrum danae*, the black darter or black meadowhawk. Black circles display mean flight date for the first quartile (the earliest fourth of flight dates), with the dashed black line and grey 95% credible interval band the fit from a Bayesian regression. Red circles display the last quartile (the latest fourth of flight dates), with the dashed red line and pink grey 95% credible interval band the fit. Note the essentially flat early-season flight ($\beta_1 = -0.01$ [$-0.13, 0.11$]) but the shift to flight later in autumn ($\beta_1 = -0.22$ [$-0.34, -0.11$]). This pattern held for many other species.

voltinism, and percent shade accounted for inter-species variation in shift in flight season breadth. (Overwintering as an egg versus as a nymph, a predictor we had expected to be associated with voltinism, was the single best predictor for shifts in flight season mean.)

Discussion

Our key findings were evidence for expanded flight season in the order Odonata, in both suborders (Zygoptera, the damselflies, and Anisoptera, the dragonflies), and in over half of the taxonomic families. By contrast, few species have advanced their emergence dates. More species have lingered, such that the overall trend for mean flight season of Odonata is now several days later. When skewness did change it was toward increased right skew, perhaps implying more late dates outside the flight season of earlier decades. That a shift in flight season breadth was the most striking result may be taken to contravene pervasive emphasis on early flight dates or advanced means. We note, however, that hypotheses about shifts to a broader flight season or to an earlier flight season are not mutually exclusive because whether one claims support for an earlier season depends on how ‘earlier’ is defined. Consider two hypothetical examples. If one used data only from the leading edge of a flight season, say the fifth percentile of flight dates, then one may conclude a forward shift if emergence dates were earlier, even though it could be that the whole season’s distribution was now skewed left and, perhaps, was broader but the mean did not change. If, by contrast,

central tendency is the response variable of focus, retreat of the trailing edge could counterbalance advance of the leading edge, yielding a potentially large increase in breadth with or without a shift in mean.

Our results do not stand in isolation. In the first study of odonate phenology relative to climate change, based on long-term data from Great Britain, [Hassall et al. \(2007\)](#) expressly posited longer flight seasons even if they found mixed support for that idea. Studies of butterfly flight season in the northeastern United States reported shifts toward longer flight seasons ([Michielini et al. 2021](#), [Zografou et al. 2021](#)), and warming can delay emergence as well as hasten emergence ([Scranton and Amarasekare 2017](#)), including in some genera of Odonata ([Woods and McGarvey 2023](#)). As more studies explore shifts in flight season breadth, we ought to consider a variety of explanations for such shifts.

Mechanisms for lengthened flight season

Often it is an open question which species-specific traits predict shifts in phenology or what mechanisms cause shifts ([Chmura et al. 2019](#)). Emergence of bees (Hymenoptera) in Colorado was associated with climatic conditions, particularly snowmelt, but other aspects of phenology were best predicted by nest location and overwinter stage ([Stemkovski et al. 2020](#)). Dietary breadth and reproductive strategy correlated with shifts in an assemblage of butterflies in the northeastern United States, with polyphagous species extending flight season and emerging earlier ([Zografou et al. 2021](#)). Yet despite a plethora of identified factors, temperature has been found to be a key driver of phenology of the Odonata and across many other insect orders ([Hassall and Thompson 2008](#), [Stoks et al. 2014](#), [Cayton et al. 2015](#), [Pollard et al. 2020](#), [Grevstad et al. 2022](#), [Woods and McGarvey 2023](#)). Even so, raising ambient temperature alone may be insufficient to trigger a shift in phenology for aquatic insects because increased precipitation (an overwhelming signal in climate change forecasts for Scandinavia, for example) alters thermal mass in lentic systems irrespective of ambient temperature ([Matthews 2010](#)). In effect, coincidence of air temperature and water temperature become decoupled, especially early in a season. Moreover, temperatures in spring, summer, and autumn of the survey years and the previous year affect phenology ([Dingemanse and Kalkman 2008](#)), implying lag effects, at least for some species, and photoperiod interacts with temperature in important ways ([Stoks et al. 2014](#)).

If we nonetheless consider solely how increased temperature may broaden a flight season, then we must consider various mechanisms, mechanisms that are not mutually exclusive and may interact. One such mechanism is voltinism, which affects insect life history profoundly ([Teder 2020](#)). In the aforementioned study of butterfly phenology ([Michielini et al. 2021](#)), an increase in the incidence of multivoltinism provided a credible link with flight season length, and the sole trait associated with phenological shifts of hoverfly (Diptera) species in Great Britain was

voltinism, in that, as with the butterflies, multivoltine species shifted most ([Hassall et al. 2017](#)). We expected a similar link because development time of odonate eggs and nymphs is shortened in warmer conditions ([Frances et al. 2017](#), [McCauley et al. 2018](#)), increasing the potential to add a generation within a year, and partivoltine species may shorten their cycle if conditions become sunnier ([Norling 2021](#)). We nevertheless found that the effect on flight season breadth of voltinism alone was weak. We instead found voltinism was a good predictor only in interaction with anthropogenic habitat and percent shade, both of which are presumed to correlate with exposure and, thus, more radiative heating.

It is unclear why voltinism by itself did not carry a stronger signal in our analyses. In ecological systems, distinctions between predictor and response are fluid: a predictor in one circumstance may be a response in another. Many such 'intermediate level' predictors exist. In our study, it may be that voltinism is not a 'pure' predictor but is itself affected directly or indirectly by factors other than that year's temperature (the putative driver we assume). One indirect effect is interannual lags. Flight date is affected by temperatures the previous year ([Dingemanse and Kalkman 2008](#)), which implies conditions when univoltine, semivoltine, or partivoltine species lay their eggs affect early emergence. Also, the British dragonflies study ([Hassall et al. 2007](#)) reported that the key species-specific trait for an advance in flight season was whether diapause occurred at the egg stage. (We corroborated this finding for shifts in flight season mean: 'overwintering as egg or nymph' was the single best predictor – the variable appeared in 100% of well-supported models. It had negligible explanatory power for flight season breadth.) Conversely, bivoltine or multivoltine species may respond to warming by initially emerging later because autumn emergence reduces the 'crop' available to hatch in spring, a mechanism used to explain a shift toward later odonate flight dates in Japan ([Doi 2008](#)) and later codified as a development trap called the 'lost generation hypothesis' ([Van Dyck et al. 2015](#)). We conclude it is likely that any relationship between voltinism and flight season breadth is contingent on other factors. One such factor may be exposure of breeding or foraging sites. A finding of a rapid shift toward shorter generation time with reduction of shade and concordant increase in sunlight ([Norling 2021](#)) suggests a role for human land use, specifically any propensity to favour open habitats over forested ones. Species that broadened their flight season were, in part, those that occupy human-modified and more open habitats (i.e. more 'weedy' species), suggesting an indirect path for voltinism-mediated increase in flight season breadth. In the end, though, it may be that mean voltinism itself is a poor proxy for evolutionary or facultative potential to add generations.

Temperature may affect flight season breadth more directly, without mediation via a shortening of generation time. For example, experimental warming of developing *Erythemis collocata* confirmed a more rapid development and earlier emergence but found, too, that fewer individuals

emerged on a given day and emergence was spread out more across the season (McCauley et al. 2018). Likewise, shorter winters led to protracted emergence in the bee *Osmia lignaria* (Bosch and Kemp 2000) and extended emergence by > 15 days in an assemblage of freshwater insects (Baranov et al. 2020). A warming-induced protraction of emergence would lengthen a flight season without a switch in voltinism.

Another mechanism that could lengthen flight season without altering voltinism is cohort splitting, a phenomenon in which, say, an insect population that emerges more-or-less simultaneously bifurcates into groups that develop or mature at different rates (Crowley and Hopper 2015). Cohort splitting occurs, for example, if most individuals emerge in late spring but some adults reproduce immediately while other adults reproduce in late summer. Cohorts of the damselfly *Lestes viridis* split differently along an elevational gradient in Algeria. Flight season shortened with increased elevation. Cohorts overlapped in colder conditions at high elevation, whereas cohorts in warmer conditions at low elevation were phenologically disjunct (Amari et al. 2019). Hence, warming could lengthen flight season when cohorts are split (Braune et al. 2008). Cohort splitting need not involve shifts in voltinism, yet developmental plasticity in response to warming may trigger shifts in voltinism that could split cohorts, and various ecological interactions, from competition to predation, affect the incidence of cohort splitting (Watts and Thompson 2012).

Potential consequences

It has been suggested that phenological shifts will decouple ecological systems, but evidence is mixed (Renner and Zohner 2018, Iler et al. 2021). Even so, ways in which earlier or later flight of dragonflies and damselflies could affect freshwater ecosystems involve their place in the food web (Bried et al. 2020). All species of Odonata are predators, both as nymphs and as adults, as well as prey for a variety of animals. Any change in when a predator appears in a system could send ripples through a food web if the timing of the prey does not change concomitantly (Patten et al. 2019).

Beyond timing of flight season itself, the extent to which generation time shifts will have even larger consequences. Various insect species have responded to warmer summers by shortening their generation time (Traill et al. 2010, Forrest 2016, Forrest et al. 2019). Models predict the same pattern in Odonata (Braune et al. 2008). A swarm of predators emerging twice a year instead of once a year doubtless will affect freshwater systems in profound and surprising ways. If chiefly generalist or ecologically tolerant species drive this pattern, then research into specific effects of those species, especially in the autumn (Gallinat et al. 2015), will go far to inform and fine tune forecasts of long-term consequences.

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Author contributions

Michael A. Patten: Conceptualization (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Brittany Rae Benson:** Conceptualization (supporting); Data curation (lead); Methodology (supporting); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8pk0p2nsw> (Patten and Benson 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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