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A temperature-driven modelling framework for mosquito seasonal phenology and generational dynamics in temperate urban environments of the Balkan region

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Abstract. Understanding the seasonal dynamics of mosquito populations in temperate urban environments is essential for predicting vector emergence, estimating generational turnover, and anticipating climate-driven shifts in phenology. This study presents a temperature-driven modelling framework that integrates degree-day accumulation, photoperiod-controlled seasonal activity, and density-dependent population regulation to simulate the seasonal development of *Culex pipiens* L. and *Aedes albopictus* (Skuse) under temperate Balkan conditions. The model distinguishes between two biologically meaningful metrics: developmental generations (egg-to-adult completion) and realised reproductive generations (egg-to-adult-to-first oviposition), thereby linking phenology to reproductive potential. Seasonal activity is constrained using ecologically defined thresholds of mean daily temperature and daylength, ensuring biologically realistic onset and termination of development. A carrying capacity term is incorporated to prevent unrealistic exponential growth and to approximate density-dependent regulation in urban habitats. Using a typical temperate climatic year, we evaluate baseline seasonal dynamics and explore a +1°C warming scenario to quantify shifts in active season length and generational turnover. Results indicate that modest temperature increases can extend the active window and increase the number of completed generations, particularly when reproductive maturation is considered. The proposed framework provides a transparent and transferable tool for assessing mosquito seasonal dynamics in temperate regions and can be readily extended to incorporate additional environmental drivers where required.

Key words: degree-day model, generational turnover, reproductive generation, photoperiod constraint, temperate climate, urban ecology.

Introduction

Mosquitoes (Diptera: Culicidae) are key components of freshwater–terrestrial ecotones and represent ecologically and epidemiologically important insect groups across temperate regions. Their seasonal population dynamics emerge from the interaction between physiological temperature dependence and environmental constraints that regulate development, reproduction, and survival. In temperate climates, seasonal timing determines not only abundance but also generational turnover and the length of the active trans-mission window (Ciota et al., 2014; Ewing et al., 2016).

Temperature acts as the primary driver of developmental progression in poikilothermic organisms. Within biologically relevant ranges, developmental rates increase predictably with temperature and can be described using thermal summation approaches such as degree-day models (Damos & Savopoulou-Soultani, 2012; Gu & Novak, 2006). Degree-day frameworks remain widely applied in mosquito phenology studies because they provide transparent, interpretable estimates of generation timing under fluctuating field conditions (Delatte et al., 2009). Experimental and field-based studies consistently demonstrate that even modest temperature increases can accelerate life-cycle completion and alter seasonal population trajectories (Ciota et al., 2014; Ewing et al., 2016).

In temperate systems, photoperiod provides a stable seasonal cue that regulates diapause induction and seasonal termination. In *Culex pipiens*, diapause typically occurs in adult females, whereas in *Aedes albopictus* diapause is expressed primarily at the egg stage, facilitating winter survival and geographic expansion into cooler regions (Haba & McBride, 2022; Paupy et al., 2009). Photoperiodic control therefore constrains late-season development even when short-term thermal conditions remain permissive, and it defines biologically realistic seasonal boundaries in phenological modelling.

Across Europe and the Balkan Peninsula, recent syntheses document the continued establishment and spread of invasive container-breeding mosquitoes, including *Aedes albopictus*, under contemporary climatic conditions (Tisseuil et al., 2018). Regional studies further indicate that modest warming scenarios can shift seasonal timing and extend activity windows in temperate environments (Ebi & Nealon, 2016). These shifts are particularly relevant in urban settings, where microclimatic modification, including urban heat island effects, can locally enhance thermal conditions (Dimitrov & Mollov, 2022).

In Bulgaria and neighbouring Balkan regions, ecological investigations have documented seasonal insect dynamics and temperature variability in urban contexts, emphasizing the importance of fine-scale climatic drivers for interpreting phenological responses. Methodological approaches developed within Ecologia Balkanica have highlighted the relevance of clearly defined seasonal metrics and temperature-based thresholds in long-term ecological research (Anev et al., 2023; Petrova & Nikolov, 2023). These regional contributions underscore the need for reproducible, climate-driven frameworks that remain operationally simple yet biologically grounded.

Most existing mosquito models focus either on detailed population dynamics or on transmission potential. However, fewer studies explicitly distinguish between developmental completion (egg-to-adult) and realised reproductive completion (egg-to-adult-to-first oviposition) when estimating seasonal generation number. This distinction is ecologically important because reproducetive maturation introduces an additional thermal requirement that directly links phenology to reproductive potential rather than mere developmental progression.

The present study proposes a reproducible, temperature-driven phenological framework for temperate urban environments of the Balkan region. The model integrates degree-day accumulation above species-specific developmental thresholds and photoperiod-defined seasonal activity windows to constrain biologically plausible development. The framework is parameterised in parallel for two ecologically contrasting mosquito types: the native temperate species *Culex pipiens* and the invasive urban container breeder *Aedes albopictus*. By distinguishing between developmental generations and realised reproductive generations, the approach provides a transparent metric of seasonal amplification under moderate warming scenarios.

Using a typical temperate climatic year, the study evaluates baseline seasonal timing and examines the phenological consequences of a +1°C warming scenario. Rather than emphasising absolute abundance, the analysis focuses on shifts in generation timing and cumulative seasonal advancement, thereby highlighting the progressive intra-seasonal amplification that may arise even under modest climatic change in temperate Balkan environments. This study aims to quantify the seasonal timing and phenological advancement of realised reproductive generations under baseline and warming conditions.

Materials and methods

Study framework and climatic inputs

This study develops a temperature-driven phenological framework to describe seasonal mosquito dynamics under temperate Balkan climatic conditions. The modelling framework is based on established degree-day approaches widely used in insect phenology studies (Damos & Savopoulou-Soultani, 2012; Delatte et al., 2009; Gu & Novak, 2006), with modifications introduced to estimate realised reproductive generations. The model operates at daily temporal resolution and uses a representative "typical year" composed of mean daily temperature values (T_{mean}). Latitude was fixed at 42.5°N to calculate astronomical daylength and define seasonal photoperiod constraints.

Daily climatic inputs included:

- mean daily air temperature (T_{mean}),
- day of year (*DOY*),
- calculated daylength (hours).

No precipitation or atmospheric moisture variables were included in the present model version, as the objective was to isolate the phenological effects of temperature and photoperiod.

Definition of active season

Developmental accumulation was restricted to biologically plausible seasonal windows. A day was considered climatically active when:

- $T_{mean} \geq 10°C$
- Daylength > 11 hours.

These thresholds approximate the onset of sustained mosquito activity in temperate Balkan environments and prevent unrealistic early-spring or late-autumn thermal accumulation.

Outside the active window, cumulative thermal units were reset to zero for the subsequent season. This reset mechanism represents seasonal phenological separation rather than population extinction.

Thermal development model

Developmental progression was modelled using a linear degree-day (*DD*) approach. Daily degree-days were calculated as:

$$\boldsymbol{DD = \max(0, T_{mean} - T_0)}$$

where T_0 represents the species-specific lower developmental threshold. When $T_{mean} < T_0$, development ceased ($DD = 0$).

Cumulative degree-days (Cum *DD*) were obtained by summing daily *DD* values within the active season.

A developmental generation (*Gen*) was considered complete when cumulative thermal units reached the species-specific developmental constant K_{dev}.

Realised reproductive generations

In addition to developmental completion (egg-to-adult), the model estimates realised reproductive generations (Real_Gen), defined as egg-to-adult-to-first oviposition. This metric incorporates an additional pre-oviposition thermal requirement ($K_{preovip}$). Thus:

$$\boldsymbol{K_{real} = K_{dev} + K_{preovip}}$$

A realised reproductive generation was recorded once cumulative thermal units reached K_{real}. This distinction allows direct assessment of phenological progression linked to reproductive output rather than developmental completion alone.

Species parameterisation

The framework was parameterised for two ecologically contrasting mosquito types characteristic of temperate Balkan urban systems (Table 1).

Table 1. Thermal developmental parameters for *Culex pipiens* and *Aedes albopictus.*

Parameter	*Culex pipiens*	*Aedes albopictus*
Lower developmental threshold, °C	5.5	6.0
Developmental constant K_{dev}, DD	199.5	190
Pre-oviposition requirement $K_{preovip}$, DD	60	50
Total reproductive requirement K_{real}, DD	259.5	240

Climate scenario

To evaluate phenological sensitivity to moderate warming, a uniform +1°C scenario was applied to all daily temperature values:

$$\boldsymbol{T_{mean}^{+1^oC} = T_{mean} + 1}$$

All other parameters remained unchanged. The analysis compared baseline and warming scenarios in terms of:

- timing of realised reproductive generations,
- cumulative seasonal advancement,
- total number of completed realised generations,
- active season length.

Data processing and visualisation

Daily calculations and cumulative metrics were implemented in Microsoft Excel. Generation timing was extracted as the first *DOY* at which each realised reproductive generation was completed ($k \geq 2$). Seasonal advancement under warming was quantified as the difference in *DOY* between baseline and +1°C scenarios.

Results are presented as seasonal developmental trajectories and generation timing plots, allowing direct visual comparison of phenological displacement under moderate warming.

Results

Seasonal dynamics under baseline climatic conditions

Under baseline temperature conditions, both species exhibited (*Culex pipiens* and *Aedes albopictus*) clearly defined seasonal windows constrained by thermal thresholds and photoperiod limits. Developmental accumulation initiated in late spring, followed by progressive completion of realised reproductive generations through summer and early autumn.

In *Culex pipiens*, the first realised reproductive generation beyond overwintering conditions (k ≥ 2) was completed on *DOY* 131. Subsequent generations accumulated progressively at decreasing temporal intervals during peak summer temperatures. The highest generation number under baseline conditions reached k = 12, completed on *DOY* 274. After this point, declining daylength and temperature prevented further reproductive completion within the same seasonal cycle (Fig. 1). The figure displays two seasonally varying trajectories. The stepwise (orange) curve expresses the cumulative number of realised reproductive generations of *Culex pipiens* completed during the year, whereas the other curve (blue) represents mean daily air temperature in °C and its short-term fluctuations, which regulate the rate of thermal accumulation. Development occurs only within the defined active season (Tmean ≥ 10°C; daylength > 11 h).

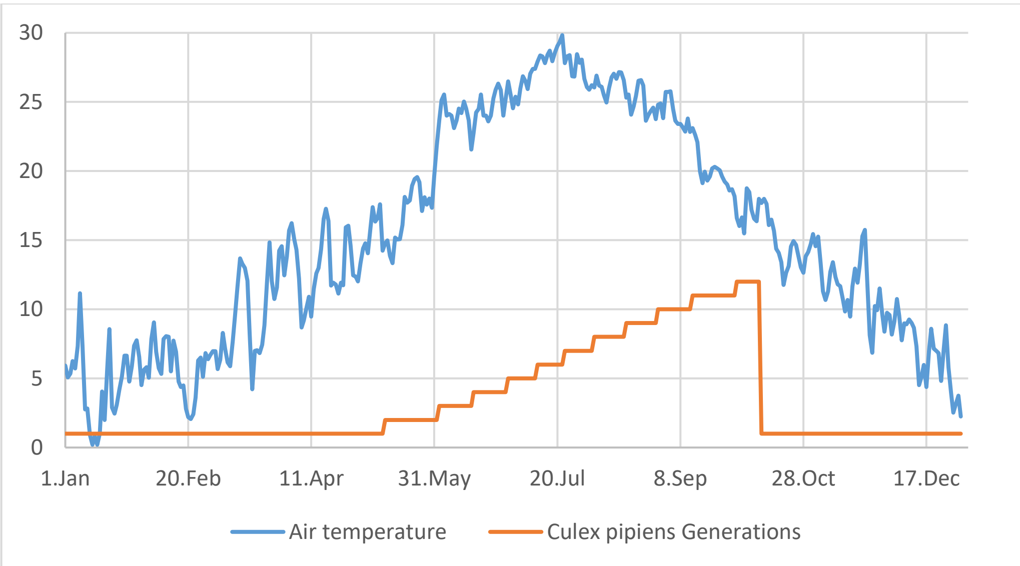


Fig. 1. Seasonal accumulation of realised reproductive generations in *Culex pipiens* under baseline climatic conditions.

The seasonal profile shows that generation turnover accelerated during mid-summer, when temperature remained consistently above the developmental threshold. However, progression slowed toward the end of the season as photoperiod approached the defined constraint.

Aedes albopictus exhibited a broadly similar seasonal structure but with slightly shifted timing. The second realised reproductive generation (k = 2) was completed on *DOY* 131 under baseline conditions. Generational intervals were marginally shorter during early summer compared to *Culex pipiens*, reflecting species-specific thermal requirements (Fig. 2.). The figure displays two seasonally varying trajectories. The stepwise (orange) curve expresses the cumulative number of realised reproductive generations of *Aedes albopictus* completed during the year, whereas the other curve (blue) represents mean daily air temperature in °C and its short-term fluctuations that govern thermal accumulation. Seasonal progression follows species-specific thermal requirements within the defined active season (T_{mean} ≥ 10°C; daylength > 11 h).

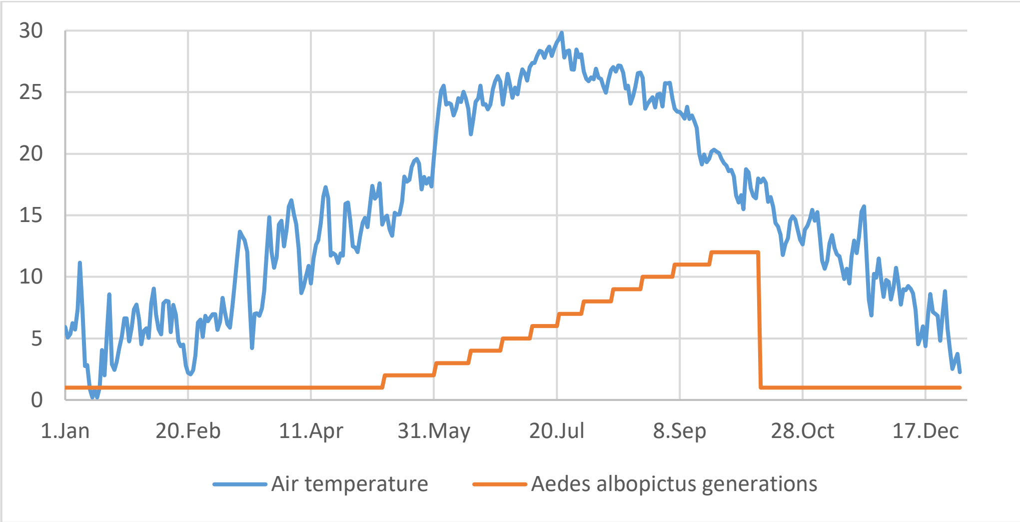


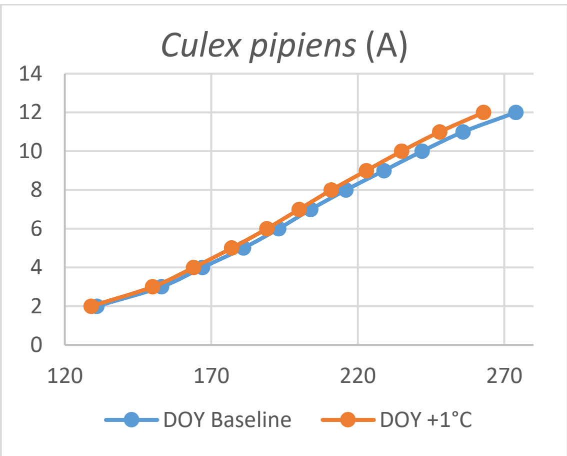
Fig. 2. Seasonal accumulation of realised reproductive generations in *Aedes albopictus* under baseline climatic conditions.

The maximum realised reproductive generation under baseline conditions reached k = 12, completed on *DOY* 264. Seasonal termination occurred earlier relative to cumulative thermal accumulation due to photoperiod restriction.

Overall, both species completed 12 realised reproductive generations under baseline climatic conditions, although their intra-seasonal timing patterns differed modestly.

Phenological response to +1°C warming

Application of a uniform +1°C warming scenario produced systematic advancement in the timing of successive realised reproductive generations for both species (Fig. 3). Points indicate the first day of year (*DOY*) at which each realised reproductive generation (k ≥ 2) is completed. The +1°C scenario advances successive generations relative to baseline conditions, with increasing displacement toward the end of the active season.

(A) 

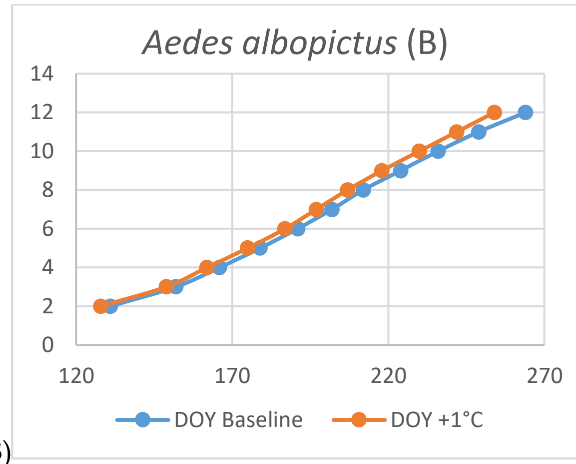
(B) 

Fig. 3. Seasonal timing of realised reproductive generations under baseline and +1°C scenarios: (A) *Culex pipiens*; (B) *Aedes albopictus*.

Progressive seasonal advancement

In *Culex pipiens*, warming advanced the second realised generation by 2 days (*DOY* 129 vs 131). The magnitude of advancement increased progressively for later generations, reaching an 11-day shift by generation 12 (DOY 263 vs 274). This pattern indicates cumulative intra-seasonal acceleration rather than uniform temporal displacement.

A comparable progressive advancement occurred in *Aedes albopictus*. The second generation advanced by three days (*DOY* 128 vs 131), while the twelfth generation advanced by ten days (*DOY* 254 vs 264). As in *Culex pipiens*, the degree of advancement increased toward the end of the active season.

Additional generation under warming

Under the +1°C scenario, both species completed an additional realised reproductive generation (k = 13), which was not achieved under baseline conditions. In *Culex pipiens*, generation 13 was completed on *DOY* 281. In *Aedes albopictus*, generation 13 was completed on *DOY* 270.

Thus, moderate warming did not merely shift seasonal timing but also expanded total realised reproductive output within a single climatic year.

Active season length

The warming scenario extended the defined active season by three days for both species under the applied thermal and photoperiod thresholds. Although this extension was numerically modest, it contributed to cumulative generational advancement and enabled completion of an additional reproductive cycle.

Comparative species response

Both species displayed qualitatively similar phenological responses to moderate warming. However, the rate of progressive advancement across successive generations differed slightly, with Culex pipiens exhibiting a marginally larger late-season shift for higher generation numbers.

These results demonstrate that even small temperature increases can generate cumulative intra-seasonal acceleration in realised reproducetive generations, thereby amplifying seasonal turnover beyond what would be inferred from early-season shifts alone.

Discussion

The present study demonstrates that moderate warming can produce progressive intra-seasonal advancement in realised reproductive generations of temperate mosquitoes. Rather than generating a uniform temporal shift, a +1°C increase systematically advances successive generations, with the magnitude of displacement increasing toward the end of the active season. This cumulative acceleration represents a key phenological amplification mechanism.

Temperature governs developmental rates in poikilothermic organisms, and degree-day frameworks reliably capture this relationship within suboptimal thermal ranges (Ciota et al., 2014; Damos & Savopoulou-Soultani, 2012). However, most temperature-driven mosquito models emphasise developmental completion or vectorial capacity rather than explicitly distinguishing between developmental and realised reproductive generations. By incorporating a pre-oviposition thermal requirement, the present framework links phenological timing directly to reproductive potential rather than developmental turnover alone.

The results show that even a modest warming scenario advances early-season generations by only a few days, yet this initial displacement accumulates across successive cycles. Later generations therefore experience progressively greater advancement, reaching shifts of approximately 10–11 days by the end of the active season. This pattern highlights those small early thermal advantages compound through repeated life-cycle completion, producing nonlinear seasonal amplification.

Importantly, warming enabled completion of an additional realised reproductive generation within the same climatic year. Although the active season extended by only three days under the applied thresholds, cumulative thermal acceleration permitted a full additional reproductive cycle. This research illustrates that generational turnover may increase even when changes in season length appear numerically modest.

Both *Culex pipiens* and *Aedes albopictus* exhibited qualitatively similar responses to warming, indicating that progressive phenological acceleration may represent a general property of temperature-driven seasonal systems. Nevertheless, minor interspecific differences emerged in the rate of late-season advancement. These differences likely reflect species-specific thermal constants and developmental thresholds rather than structural model assumptions.

The incorporation of photoperiod constraints prevented unrealistic late-autumn accumulation under anomalously warm conditions. Photoperiod thus functions as a seasonal boundary regulator, ensuring biologically plausible termination of development even when temperature remains permissive. This interaction between thermal aceleration and photoperiod limitation defines the effective seasonal envelope within which progressive advancement operates.

The study intentionally focuses on phenological dynamics rather than explicit population abundance. While increased generational turnover may imply enhanced reproductive output, absolute population size depends on additional ecological processes, including habitat availability, density dependence, predation, and control measures. The framework therefore provides a mechanistic basis for interpreting seasonal timing rather than a predictive model of abundance.

From a regional perspective, the Balkan Peninsula represents a transitional climatic zone where relatively small shifts in mean temperature may translate into measurable changes in seasonal timing. Urban microclimatic modification, including local heat island effects documented in Bulgarian cities (Dimitrov & Mollov, 2022; Ivanov, 2025), may further amplify these dynamics at fine spatial scales. The progressive nature of phenological advancement suggests that warming effects may become increasingly pronounced toward the end of the active season, potentially altering late-season ecological interactions.

Several limitations warrant consideration. The model assumes fixed developmental thresholds and thermal constants, although local adaptation may introduce variability. The use of a representative "typical year" does not capture interannual variability or extreme events. Additionally, diapause dynamics are represented indirectly through photoperiod constraints rather than through explicit stage-structured overwintering modules. Future refinements may incurporate probabilistic parameter ranges or site-specific calibration using field data.

Despite these limitations, the framework offers a transparent and reproducible approach for quantifying seasonal timing and generational displacement under moderate warming. By distinguishing developmental completion from realised reproductive completion, the model provides a biologically meaningful metric of seasonal amplification in temperate mosquito systems.

Conclusion

This study presents a temperature-driven phenological framework for assessing seasonal mosquito dynamics in temperate Balkan environments. By integrating degree-day accumulation with photoperiod-defined activity windows, the model defines biologically plausible seasonal boundaries and enables estimation of realised reproductive generation timing.

The results demonstrate that a +1°C warming scenario produces progressive intra-seasonal advancement rather than uniform temporal displacement. Successive generations occur increasingly earlier in the calendar year, and cumulative acceleration enables completion of an additional reproductive cycle despite only modest extension of the active season.

The distinction between developmental and realised reproductive generations provides a transparent metric linking phenology to reproductive potential. This approach highlights how moderate climatic changes can amplify seasonal turnover in temperate systems through cumulative life-cycle acceleration.

Beyond its predictive value for seasonal population dynamics, the framework also supports adaptive vector management. By identifying temperature-dependent thresholds associated with successive realised reproductive generations, control interventions can be aligned with real-time thermal conditions rather than fixed calendar dates. Because seasonal onset shifts under interannual climatic variability and urban microclimatic modification—including urban heat island effects documented in Balkan cities - temperature-based monitoring reduces the risk of delayed intervention during early-season developmental transitions.

Given the climatic sensitivity of transitional Balkan environments, the proposed framework offers a practical tool for comparative phenological assessment across urban sites. Future applications may incorporate interannual variability, microclimatic datasets, and field validation to refine regional predictions.

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