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## Weather - food web interactions steer the dynamics of an insect population

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## Abstract

Insect population dynamics are the result of an interplay between intraspecific competition, trophic interactions and external forces such as weather conditions, but studying how these processes combine to determine population change is challenging. We investigate mechanisms of population dynamics in a natural, low density insect population. Eggs and larvae of the noctuid moth, *Abrostola asclepiadis*, develop on its host plant during summer. The population density, and mortality, was closely monitored throughout this period during 15 years. Densities fluctuated between one and two orders of magnitude. Egg – larval developmental time varied substantially among years, with lower survival in cool summers with slower development. This was presumably due to the prolonged exposure to a large guild of polyphagous arthropod enemies. We also found a density dependent component during this period, that could be a result of intraspecific competition for food among old larvae. Dynamics during the long period from pupation in late summer through winter survival in the ground to adult emergence and oviposition the next year displayed few clear patterns and more unexplained variability, thus giving a more random appearance. The population hence shows more unexplained or unpredictable variation during the long wintering period, but seems more predictable over the summer egg-larval period. Our study illustrates how weather - via a window of exposure to enemies and in combination with density-dependent processes - can determine the course of population change through the insect life cycle.

**Keywords** Climate change, density dependence, Noctuidae, population dynamics, weather effects

## Introduction

Weather conditions are important factors in the dynamics of insect populations. Among the various weather factors known to affect insects, temperature conditions are of particular importance in temperate regions. Insects are ectotherms, and cool weather limits population growth. Temperature *directly* affects many aspects of insect life such as growth rates, survival probability, reproductive rates and flight propensity (Andrewartha and Birch 1954; Bale et al. 2002). In addition to these direct effects, weather conditions also impact insect populations *indirectly* through the web of trophic interactions (Abarca and Spahn 2021). For example, plant resources used by phytophagous insects are often affected by weather (DeLucia et al. 2012; Solbreck and Knape 2017; Hambäck 2021) thus impacting the food – herbivore link. Interactions via the natural enemy link may also be modified by weather conditions (Barton and Schmitz 2009; Barton and Ives 2014; Pepi et al. 2018)

Population dynamics are the result of this interplay between intraspecific processes, trophic interactions and external forcing from weather conditions. Hence weather effects should not be considered in isolation but in combination with other factors, particularly density dependent trophic interactions (Varley et al. 1973; Royama 1992). The combined effects of weather and web are often complex resulting in a wide range of dynamical responses depending on the specific circumstances (Ives 1995; Stenseth et al. 2002; Walther 2010; Klapwijk et al. 2012; Lawson et al. 2015; Uszko et al. 2017). Due to these complexities we still have a poor understanding how weather and future climates will affect insect population change, motivating a continued analysis of specific population systems.

Holometabolous insects have complex life cycles, and ecological effects during each life history phase may be unique (Kingsolver et al. 2011). Each phase can be seen as a time window dominated by specific interactions. Window widths wax and wane in response to

environmental conditions, with sometimes strong effects on survival. For example, the slow-growth high mortality theory, summarized by Benrey and Denno (1997), postulates that slow growth causes longer exposure to enemies resulting in higher mortality risks. Although this theory was originally proposed for insects with different development times caused by food quality changes, the same effect can be expected from developmental differences due to different weather regimes. It was also shown experimentally that temperature-induced slow growth resulted in higher enemy induced mortality (Benrey and Denno 1997).

However, showing that a larger time window of exposure to enemies increases mortality is not enough to explain change in natural populations; particularly so in insects with ecologically different life history stages. What is happening during one life history phase may be modified by processes during other stages. A grasp of processes affecting the *entire* life cycle is essential when analyzing how weather conditions affect population change (Ådahl et al. 2006; Radchuk et al 2013). This also requires a prior strong selection of variables based upon knowledge of biological and ecological conditions (Knape and de Valpine 2013).

We analyze the dynamics of a low density, non-outbreak population of a noctuid moth. The larva is monophagous, feeding on the leaves of a patchily distributed perennial herb. Earlier studies have indicated that natural enemies take a heavy toll on eggs and larvae, and that this mortality is higher during cool summers (Förare 1995b). In other words, it appeared that during cold summers the time window of exposure to enemies widened causing higher mortality. Here we develop a population model to investigate the time window effects in relation to other processes – such as density dependent effects and winter weather conditions - affecting the insect population through its entire life cycle. Previous studies are also extended by using a much larger data set (15 years compared to 6 years in the previous study).

## 97 **Materials and methods**

### 98 **Biology**

99

100 The larva of *Abrostola asclepiadis* Schiff. (Lepidoptera, Noctuidae) is monophagous on the  
 101 long-lived herb, white swallow-wort, *Vincetoxicum hirundinaria* Med. (Apocynaceae) (Fig. 1  
 102 A, D, E). The insect has a southeastern distribution in Sweden, which closely follows that of  
 103 its host-plant. It has one generation per year in Sweden (Fig. 2). Moths fly in early summer  
 104 with a peak in June. Females deposit eggs in small batches (usually 1-5 eggs) on the  
 105 underside of *V. hirundinaria* leaves (Fig. 1 B, C)). Females are good flyers and are capable of  
 106 laying more than 200 eggs. They will deposit numerous egg batches in several host plant  
 107 patches. Short hostplant individuals growing in shaded positions are preferred for oviposition  
 108 (Förare 1995b; Förare and Engqvist 1996; Förare and Solbreck 1997).

109 Eggs hatch after about ten days, and larvae need another five weeks to develop. Average  
 110 development time is thus 6-7 weeks, but there is considerable variation among years  
 111 depending on temperature conditions (see below). Larvae of the first two instars are active  
 112 day and night whereas older larvae (instars 3-5) (Fig. 1 D, E) are mainly night active. Young  
 113 larvae feed collectively making small holes in the central parts of leaves. Instar 4 and 5 larvae  
 114 concentrate their feeding on young leaves at the top of the plants. They feed singly and  
 115 consume large parts of entire leaves (Fig. 1 E). The old larvae are difficult to find during  
 116 daytime when they are hiding, but are easy to spot at night with the aid of a torch. When full-  
 117 grown, larvae leave the host plant to pupate in the soil, where they remain until adult  
 118 emergence early the next summer.

119 Several kinds of invertebrate enemy attack eggs and larvae of *A. asclepiadis*, but they are  
 120 all generalists. Eggs are attacked by two species of Hymenoptera parasitoids (*Trichogramma*  
 121 sp and *Telenomus* sp) (Fig. 1 B) as well as by many species of polyphagous predators

including ants, chrysopid larvae (Fig. 1 C), anthocorid bugs and mites. The same kinds of predators also attack young larvae. The pentatomid bug *Picromerus bidens* (L.) attacks larger larvae (Fig. 1 F). Tachinid and braconid parasitoids have been reported from older larvae elsewhere but they are very rare in the study area. (Hundreds of larvae brought to the laboratory for other experiments never yielded any parasitoids.) No vertebrate predators have ever been observed and pathogens are very rarely observed (Förare 1995b). Bird predation – which may be hard to directly observe – is unlikely to be of significance. The later instars are night active and hide during the day when birds are active. Predation rates on pupae in the ground is unknown. However, as pupae are very few and spread out, only random encounters with polyphagous predators are expected.

The host plant is poisonous (Tullberg et al 2000; Kalske et al 2014) and its community of phytophagous insects is very small. Three species feed on flowers or seeds, but *A. asclepiadis* is the only leaf feeder.

### **Study area and host plant**

The study area at Tullgarn (58°57'N, 17°36'E) is situated on the coast about 50 km SSW of Stockholm. Populations of the host plant have a distinctly patchy distribution in this landscape (Solbreck 2012). Plant individuals typically form dense tussocks of from a few up to more than 100 40-80 cm tall flowering shoots. The main flowering period is June-July. *A. asclepiadis* is the only leaf feeding insect on the plant in the study area (except for rare stray specimens of polyphagous Lepidoptera species). There is one flower gall midge *Contarinia vincetoxici* Kieffer (Diptera, Cecidomyiidae) and two seed predator species, *Euphranta connexa* (Fabr.) (Diptera, Tephritidae) and *Lygaeus equestris* (L.) (Heteroptera, Lygaeidae) (Widenfalk et al. 2002; Solbreck and Knape 2017) attacking the plant.

## Sampling

Four plots were monitored 1990-2004. They had  $326 \pm 67$ ,  $712 \pm 187$ ,  $743 \pm 159$  and  $924 \pm 114$  (mean  $\pm$  SD for entire study period) shoots of *V. hirundinaria*. All plots were within a 4 km distance. The plots were inspected once every week during egg – larval periods (usually early June to mid August). The underside of every leaf was inspected for presence of *A. asclepiadis* eggs. The eggs were counted and the position of every egg batch was marked. During later visits, the fates of all eggs were noted. Eggs were classified into four groups: (1) hatched, (2) parasitized (blackened), (3) predated (disappeared or sucked out or with chewing holes different of the openings of hatched eggs) and (4) inviable.

Last instar larvae (stage V) were counted at night when they are active and easy to spot in the light of a torch. The search was guided by observations of leaf damage and larval droppings, as well as by earlier observations of the positions of IV instar larvae. When a last instar larva was encountered it was marked with a felt pen so as not to be double-counted on later visits. Egg and larval totals were calculated for each plot and year (Appendix 1). For a detailed discussion of measurement accuracies, see Appendix 2.

## Weather factors

Our choice of weather factors (or tokens thereof) to be considered in the analysis is based upon previously published studies (Förare 1995a; 1995b; Förare and Engqvist 1996; Förare and Solbreck 1997) as well as on ten additional years of field observations (CS unpubl.). These observations mainly pertain to the period from egg laying until the last days of larval life. In particular it was observed that cool weather during the egg-larval period seemed to

increase predation by extending the time span for exposure to enemies. Observations pertaining to the long inactive pupal period, on the other hand, are few because of the combination of low population density and the hidden life of pupae in the soil. Finally, observations of the adult flight period are reflected in the patterns of egg laying.

*The egg – larval development period (summer period)*

Temperature is a prime weather factor affecting eggs and larvae. Laboratory rearings had shown a very tight relationship between temperature and larval development rate for the range of temperatures encountered in the field (Förare and Engqvist 1996). Field observations further indicate that *air* temperature (rather than the amount of exposure to sunshine) is the main factor affecting development time. Eggs are laid under leaves primarily in shaded sites and large larvae are largely night active and hiding during the day.

However, there is an issue regarding the choice of time period when using standard monthly mean temperature data, because development takes place during different periods in different years. Data on first egg laid varied by about one month (June 7 to July 8), and of first fifth instar larva by almost two months (July 14 to September 10), (cf Fig. 4). In a preliminary analysis we found that mean temperature for the specific days of development each year explained more of the variation than data for specific months (only July temperatures contributed). As the insect itself can be regarded as the best thermometer of microclimatic conditions, we have instead chosen to use development time *per se* as a token for temperature conditions in our models. However, for comparison we also provide results when using mean June and July temperature instead of development time.

Egg – larval development time was calculated as the difference between the date of the **first** observed egg and the **first** observed last instar larva (in any of the plots). The reason for using first observations of eggs/larvae rather than mean or median times are that they are easily observed. There are generally no single eggs or larvae appearing well before the others.



Furthermore, because eggs are deposited and large larvae are formed over a long period of time mean/median dates of deposition become more variable and less accurate.

#### *The pupal to adult period (winter period)*

We envisaged two possible weather factors that might affect overwinter survival of pupae: 1) Winter minimum temperature. Very low temperatures could potentially cause freezing of pupae. 2) The duration of the period with snow covered ground. This might, for example, facilitate predation on pupae by winter active arthropod predators or small mammals. On the other hand, snow cover acts as an insulation against cold and it could potentially shield pupae from winter lows.

Both adult emergence and flight are likely affected by temperature. For example, high temperatures are likely to provide more nights with good flight conditions resulting in more eggs laid. In our analysis we used average May-June air temperature.

In summary the following factors were analyzed. For the egg – larva period (summer period): Egg – larval development time was used as a token for air temperature. For the overwintering period: Winter minimum temperature, number of days with snow cover and mean air temperature for May-June. Standard meteorological data were obtained from Stockholm, about 50 km to the north of the study area.

#### **Data treatment and population model**

We pooled data from the four patches because most of the individuals come from a single patch, and the remaining patches had too few individuals to reliably fit our population model below. For reference estimates from separate analyses of data from single patches are however provided in Table 1. Insect abundance was measured at three points in the life cycle

of *A. asclepiadis*, namely, eggs laid, eggs hatched (=first instar larvae produced), and fifth instar larvae produced (Fig. 2).

In a preliminary analysis possible time trends or density dependence in the different egg mortalities were investigated. However, there were no indications of non-random patterns, in the various egg mortality factors, and hence the different egg mortalities were not considered in the further analysis.

For the population model we therefore just used two of the annual measures namely, the egg stage (E) soon after oviposition, and the final larval stage (L) approximately 1-2 months later (Fig. 2). We thus model the population process in two steps per year. The first encompasses most of egg-larval stages, and the second (mainly) the pupa - adult stages until oviposition.

#### ***Survival during egg – larval period***

Given that there were  $E_t$  eggs in the beginning of the season in year  $t$  we model survival to the final larval stage using a binomial model

$$L_t \sim \text{Binomial}(E_t, s_t)$$

where  $s_t$  is the probability of survival over the entire period. The binomial distribution accounts for demographic stochasticity in survival. We model the survival probability as a function of the observed annual development time, the number of eggs laid to account for possible density dependence, and a random year effect to account for additional environmental stochasticity. We introduce these variables using a complementary log-log link for the probability of eggs to die before reaching the final larval stage.

In terms of survival, the equation is

$$s_t = \exp(-\exp(a + b \log E_t + c \log d_t + \epsilon_t)) \quad \text{Eq 1}$$

where  $a$  is an intercept,  $b$  a slope for density dependence,  $d_t$  is the estimated development time in year  $t$  and  $c$  its slope coefficient, and  $\epsilon_t$  is a normally distributed random year effect. Under this model, mortality increases and survival decreases as the coefficients increase. For instance, a positive  $b$  would indicate negative density dependence. The choice of a complementary log-log link and the inclusion of the logarithm of development time for survival implies that the survival probability  $s_t$  corresponds to the survival probability up to time  $d_t$  under a Weibull hazard rate (Pinder et al. 1998). This hazard is a power function of time with shape determined by the parameter  $c$  ( $c=1$  corresponds to a constant hazard) and scale determined by the other covariates and the random effect.

### ***Pupal – adult survival to oviposition***

The second part of the model involves the process from [the latter part of] last instar larvae in the autumn of year  $t$  to the number of eggs laid the following year. Thus, it may be seen as a simple model of the combined effect of several subprocesses in the development from the final larval stage, through the overwintering pupal and emerging adult stages. The per capita productivity is modelled linearly on the log scale with an intercept term, a slope for the log number of larvae describing density dependence, and a random year effect. To account for demographic stochasticity in productivity we use Poisson distributions. The second submodel therefore is

$$E_t \sim \text{Poisson}(L_{t-1} \exp(\mu + f \log L_{t-1} + \eta_t)) \quad \text{Eq 2}$$

where  $\mu$  is an intercept,  $f$  a slope for density effects and  $\eta_t$  is a random year effect.

In separate analyses we investigated effects of potential weather covariates on wintering dynamics. In a first model we used winter minimum temperature and the number of snow-days as covariates in the exponent of eq (2), and in a second model we used May and July temperature as a covariate potentially affecting flying of adults before egg laying. Since the estimates did not show any clear responses to these covariates, these models are not considered further, but the corresponding estimates are provided in Table 1.

We fitted models in a Bayesian framework using MCMC sampling via the JAGS software (Plummer 2017). All parameters were given vague prior distributions, and convergence of MCMC chains was assessed through visual inspection of parameter traceplots. [Tentative: The code for the analysis is provided in Supplement X]

## Results

The range of population fluctuations in egg and larval abundances was between one and two orders of magnitude (Fig. 3). The mortality was higher during the larval stages than during the egg stage. Almost all mortality during the egg stage was due to arthropod predators and Hymenoptera parasitoids (Appendix 1). Since larval parasitoids and pathogens are very rare in the study area predators are likely to be the dominating enemies of larvae (see Discussion).

The duration of the egg – larval development period varied considerably among years (Fig. 4). Development time had a strong effect on interval mortality, with higher mortality in summers with slow development (Fig. 5, Table 1). The coefficient for development time was estimated to 1.0 (0.6, 1.5), consistent with a constant mortality hazard during larval

development. Density dependent factors also seem to act during this period (Fig. 6A, Table 1), but estimates of density dependence are sensitive to sampling or observation errors e.g. Freckleton et al 2006; Knape 2008).

For the period from last instar larvae to eggs in the following year, parameter estimates suggest a density dependent pattern in the production of eggs (Fig 6B). There was further a large amount of unexplained variation in the dynamics over this period (Fig. 6B, Table 1). Weather effects during this period of the life cycle were uncertain with credible intervals overlapping zero (Table 1).

Comparing forward predictions from the model to observed data (Fig. 7) indicates reasonable model performance, but with a few observations in the tails of the predictive distribution.

Simulating from the fitted model with only the sequence of weather data and the population start data from 1990 as inputs shows that the model captures essential aspects of population behaviour, albeit with considerable variation around medians (or means) (Fig. 8), and with populations going extinct in some simulations.

## Discussion

### The dynamics of *A. asclepiadis*

A central question with regard to population change is to explore the mechanistic links between population dynamics and climate variability (Stenseth et al. 2002; Boggs and Inouye 2012). We develop and analyze a model of the dynamics of a noctuid moth population based upon long-term field data. The life cycle is divided into two phases (1) summer survival of eggs and larvae, and (2) autumn – winter – spring survival followed by spring reproduction. Our study suggests that summer weather effects are important. They seem to be mainly indirect, operating via a window of vulnerability. Slower development of eggs and larvae at

lower temperatures leads to an extended exposure to mortality risks. Density dependent processes seem to modify these weather-induced fluctuations. During the rest of the life cycle there were larger unexplained fluctuations with no clear weather effects.

Many arthropod natural enemies attack the immature stages of *A. asclepiadis*. They are of different sizes and feeding habits and they all seem to be generalists or at least oligophages (Förare 1995a, b). A detailed account of egg mortalities (Appendix 1) shows that polyphagous predators form the dominating mortality factor, with a strong contribution by egg parasitoids in certain years. We have less precise information on larval mortality factors, but we know that parasitoids and pathogens are absent (or at least very rare) in the study area (Förare unpubl). We also know that several of the egg predators, for example ants, chrysopid larvae and anthocorid bugs also attack and kill young larvae. Insect predators, such as pentatomid bugs, attacking the larger larvae have often been observed in the plots. Bird predation is unlikely to be of significance since the later larval stages are night-active and well concealed during the day.

Due to its very low population density across the landscape *A. asclepiadis* is undoubtedly a minor part in the diets of enemy populations. Thus, it is unlikely that enemy densities are numerically linked to *A. asclepiadis* dynamics. We hence envisage a direct and diffuse pressure by several arthropod enemy species, the effect of which is dependent on the length of exposure.

There do not seem to be any important *direct* effects of temperature during the egg – larval period. In rearing experiments encompassing a range of naturally encountered temperatures there were no clear differences in egg or larval mortalities (Förare 1995a). There are effects of temperature on pupal weight, but they are small for natural conditions (Förare 1995b). The dominating weather effect on *A. asclepiadis* populations during the summer therefore seems to be the indirect effect on the window of vulnerability to enemies.

The apparent density dependence observed during the egg – larval period is surprising in light of the very low incidence of defoliation observed in the field (Förare 1995a, b). Although occasional local defoliations have been reported for example in Finland (Leimu and Lethilä 2006), we have not seen any extensive defoliations during the last 40+ years in our study areas in Sweden. If the statistical density dependence found in our analyses indeed reflect effects of direct competition a closer examination of oviposition behaviour and conditions at the end of the larval period can solve this apparent paradox. Female moths show an oviposition preference for small and isolated plants in shaded positions (Förare and Engqvist 1996). Many larvae thus wind up on small individual plants isolated on the scale of a meter or so, and may thus experience competition for food on a very local scale (Fig. 2 G). This effect is strengthened late in summer when leaves start to yellow and fall off. Numerous field observations lend credibility to this idea of small-scale intra-specific competition for food. Shortage of food for the larvae seems to occur in many populations of Lepidoptera (Dempster 1983). It need not be due to an absolute shortage of food, but simply a result of an inability of the insect to find it in time (Andrewartha and Birch 1954). Since measurement error could lead to exaggerated estimates of density dependence, we explore this possibility in Appendix 2, concluding that errors are likely to be fairly small in our study. However, we cannot entirely rule out that they are affecting our density dependence estimates.

Interspecific competition in this *A. asclepiadis* population is highly unlikely since the host plant is poisonous (see above) and no other insects feed on its leaves (except some polyphagous species on rare occasions). Nor do any vertebrates feed on its green leaves.

During the long period (9-10 months) from mature larva in late summer until egg laying in early summer the following year there remains considerable variation to explain. Almost all of this time is spent as a pupa (inside a cocoon) hidden in the ground. However, the period also involves the final days as a larva and the movement to the pupal site. It also involves the

spring period with adult emergence, flight and oviposition.

We found no clear effects of weather conditions (minimum temperatures or snow conditions) on *A. asclepiadis* during the winter period. This is in contrast to studies of some other Lepidoptera species where winter conditions are important (e.g. Hunter et al 2014; Roland and Matter 2016; Büntgen et al 2020). Nor could we find any clear effect of temperature during spring - early summer when moths emerge, fly and oviposit.

There is a weak density dependence during the winter which is of uncertain significance. It could be due to either immigration and/or measurement error (see Appendix 2). In this context it is interesting that our model points to a considerable risk of local extinction, which however never happened in our plots. This also suggests that extinction-prone local populations can be "rescued" in spring by migrating moths. However, this is not incorporated in our models due to the lack of explicit data about moth movements.

Predictions of egg number display more unexplained variation than predictions of the number of last instar larvae. Whether this reflects a real difference in predictability or our ignorance of some important process is uncertain. However, it illustrates that the number and specific choice of life history stages can be of importance when analysing the factors affecting population change.

### **Idiosyncrasies in the responses of insects to weather factors**

What general conclusions concerning insect population dynamics in a new climate can be drawn from our findings about *A. asclepiadis*? The population responses of insects to weather/climate seem to harbour many idiosyncrasies. As mentioned, weather can influence the dynamics of populations via multiple pathways, and can affect any stage in the life cycle (e.g. Azerefegne et al 2001). They can act indirectly via the trophic web, and interact with density dependent processes. Accordingly, generalisations with regard to weather effects on



397 insect populations are hard to find. v

398       *Abrostola asclepiadis* and the three other insect species feeding on *V. hirundinaria* in the  
 399 study area add to this list of special cases. The flower gall midge species (*Contarinia*  
 400 *vincetoxici* Kieffer) (Cecidomyiidae) fluctuates in multi-annual cycles with little connection  
 401 to any direct weather conditions (Solbreck and Widenfalk 2012). Populations of the seed  
 402 predatory fly *Euphranta connexa* (Fabr.) (Tephritidae) are strongly coupled to seed density  
 403 fluctuations, which in turn are determined by both un-lagged and lagged weather conditions  
 404 (Solbreck and Knape 2017). Finally, populations of the seed predatory bug *Lygaeus equestris*  
 405 (L.) (Lygaeidae) are affected by both un-lagged and moderately lagged direct weather  
 406 conditions as well as by lagged indirect effects via seed production, but there are no known  
 407 effects of enemies (Solbreck 1995). There are thus few commonalities in weather/climate  
 408 effects in this insect community.

409       That there are strong idiosyncrasies in responses to weather and climate is further  
 410 supported when we compare our results to the few previous studies of weather effects on  
 411 temperate region noctuids. Cool weather resulted in better host plant growth, causing a long-  
 412 term plant community - insect density interaction in larval populations of the outbreaking  
 413 moth *Cerapteryx graminis* (Danell and Ericson 1990), and an analysis of light trap catches of  
 414 12 abundant noctuid moth species in England found that populations were negatively affected  
 415 by cold and rainy winters (Mutshinda et al. 2011).

416       The problem of finding simple generalizations pertaining to weather and climate effects  
 417 on population dynamics is not limited to insects. It seems to be common among many animal  
 418 groups, as illustrated by a recent review of responses among terrestrial mammals (Paniw et al  
 419 2021). Are we left with a plethora of special cases?

420

421 **Conclusions**

We show how weather may affect an insect population indirectly through a temperature dependent window of vulnerability towards natural enemies. This process in combination with density dependent factors steers population density at the end of the summer egg - larval period. During the remaining part of the yearly life cycle (autumn, winter, spring) population density is less easily predicted, only to be funneled back towards more easily predicted densities the following summer period. Our study adds yet another mechanism by which weather conditions can affect insect populations.

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## Figure legends

Fig. 1 (A) Adult *Abrostola asclepiadis* moth. (B) Egg batches on the underside of *V. hirundinaria* leaves attacked by undetermined Hymenoptera parasitoid, and (C) by predatory lacewing (Neuroptera) larva. (D) Third instar larva chewing a hole in a leaf and (E) a fifth (last) instar larva chewing large chunks off leaves. (F) Predatory bug (*Picromerus bidens*) (Pentatomidae) with a newly killed last instar larva. (G) Two last instar larvae competing for remaining leaf late in summer. Photographs by Bert Gustafsson (A), Jonas Förrare (B, C, F) and Christer Solbreck (D, E, G).

Fig. 2. Life cycle of *A. asclepiadis*. Egg – larval development takes place on the host plant during June – August (September). When larvae are mature they wander some meters and enter the soil where they pupate inside cocoons. They remain in the soil for about nine months. Adult moths emerge in late May June. They are strong fliers frequently moving between host plant patches. Red arrows indicate life stages monitored:  $N_e$  = number of eggs laid,  $N_l$  = number of eggs hatched, and  $N_v$  number of larvae entering the final (fifth) instar. The filled arrows indicate the two stages used in the main statistical analysis.

Fig. 3. The numbers of eggs laid, eggs hatched and last instar larvae of *A. asclepiadis* 1990 – 2004.

Fig. 4. Days (after May 1) of first egg and first last instar larva observed 1990 - 2004.

Fig. 5. Expected survival probability for the egg – larval period in relation to development



time. Calculations made under median value for egg number (374). Shaded area shows 50% intervals.

Fig. 6. A) Expected survival probability for the egg – larval period and B) per capita egg production for the late larva – adult periods in relation to initial densities. In A development time has been fixed to its median value (42 days). The shaded areas show 50% intervals.

Fig. 7. Forward model predictions of egg abundance using A) the number of larvae in the previous year or B) the number of eggs in the previous year as the starting point, and of larval abundance using C) the number of eggs the same year or D) the number of larvae the previous year. Predictions include observed values of weather variables and larval development times. Lines show 50 % prediction intervals.

Fig. 8. Simulations of (A) egg densities and (B) larval densities from the fitted model. Egg density in 1990 was used to start the simulations. Observed egg - larval development times and weather variables, but not observed egg and larval densities after the starting egg density, were used to propagate the model simulations forward in time. The hatched line gives the mean value and the continuous line the median. The shaded areas show the 50% prediction intervals. Black dots show measured data.

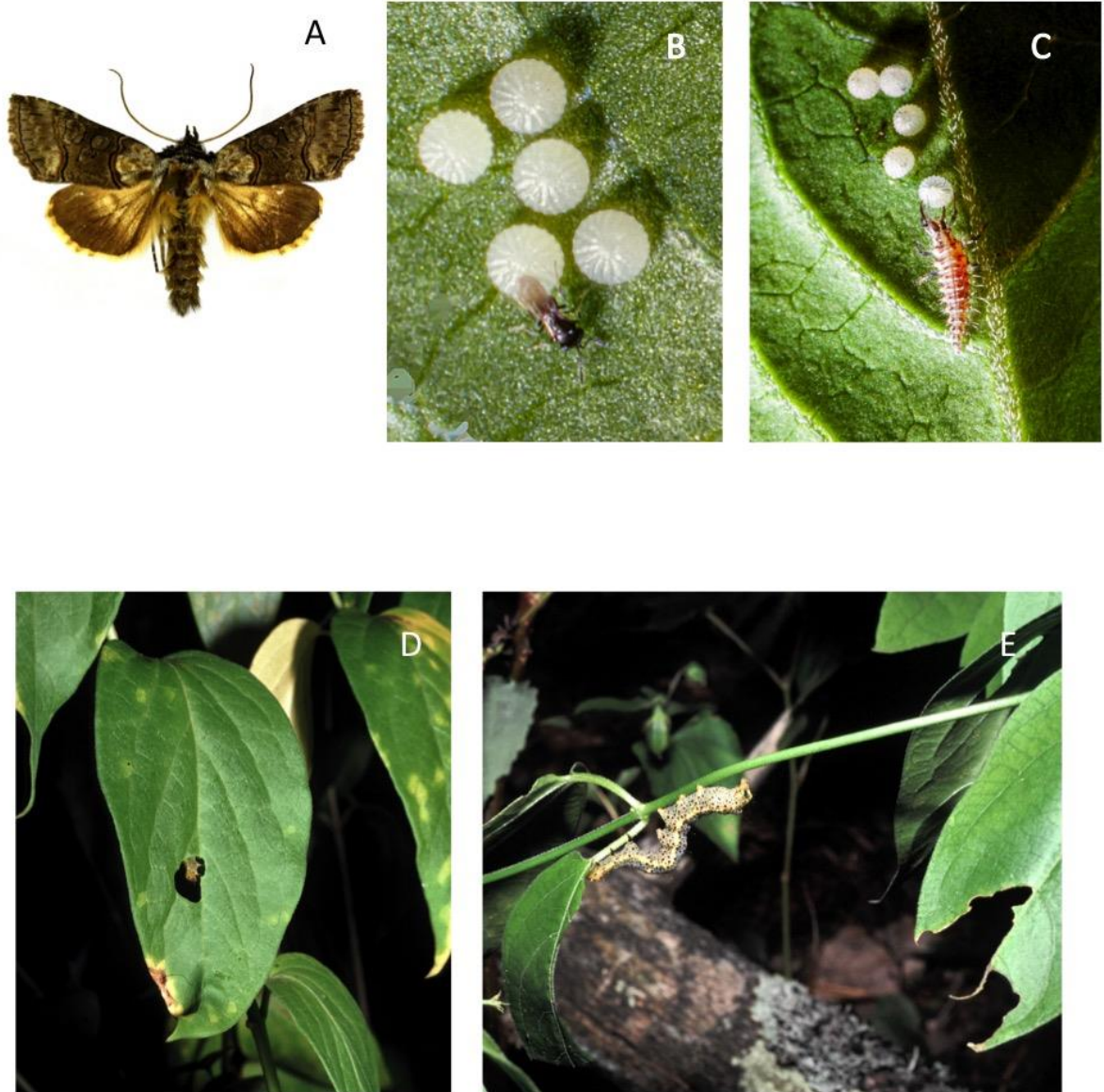
Table 1. Parameter estimates of the models.

Parameter	Parameter meaning	Estimate (95% HPD interval)	Data from patch T40A only	Data from patch T23 only	Data from patch T14 only	Data from patch T9 only	Pooled data, with winter covariates	Pooled data with spring covariate	Pooled data, temperature, instead of development time
a	intercept for hazard rate	-3.8 (-5.8, -1.9)	-3.4 (-5.8, -1.0)	0.0 (-4.1, 3.1)	-2.9 (-7.6, 1.7)	-6.4 (-9.5, -3.1)	-3.7 (-5.7, -1.7)	-3.7 (-5.5, -1.8)	1.11 (-1.15, 3.49)
b	slope for ‘density dependence’	0.20 (0.07, 0.32)	0.18 (0.02, 0.33)	0.12 (-0.07, 0.31)	0.61 (0.25, 1.00)	0.31 (0.13, 0.47)	0.20 (0.07, 0.32)	0.20 (0.07, 0.31)	0.15 (-0.06, 0.35)
c	slope for development time	1.0 (0.6, 1.5)	1.0 (0.4, 1.5)	0.3 (-0.6, 1.4)	0.6 (-0.6, 1.9)	1.7 (0.9, 2.4)	1.0 (0.5, 1.5)	1.0 (0.6, 1.4)	
$\sigma_\epsilon$	SD for random year effect	0.16 (0.09, 0.27)	0.18 (0.10, 0.30)	0.11 (0.00, 0.59)	0.10 (0.00, 0.47)	0.18 (0.02, 0.41)	0.16 (0.09, 0.27)	0.16 (0.09, 0.26)	0.29 (0.18, 0.45)
	Slope for summer temp on larval survival								-0.04 (-0.17, 0.07)
$\mu$	intercept	4.6 (4.0, 5.3)	4.6 (3.8, 5.4)	3.2 (2.0, 4.4)	1.9 (0.9, 2.8)	4.3 (3.2, 5.4)	4.4 (2.7, 6.0)	3.1 (0.6, 5.7)	4.6 (4.0, 5.2)
f	slope for ‘density dependence’	-0.41 (-0.66, -0.17)	-0.43 (0.80, -0.09)	0.28 (-2.56, 3.05)	-0.62 (-2.57, 1.37)	-0.62 (-1.28, 0.07)	-0.43 (-0.74, -0.12)	-0.50 (-0.76, -0.23)	-0.40 (-0.65, -0.16)
$\sigma_\eta$	SD for random year effect	0.49 (0.33, 0.76)	0.60 (0.39, 0.96)	0.93 (0.32, 2.18)	1.06 (0.53, 1.99)	0.86 (0.52, 1.52)	0.52 (0.34, 0.83)	0.47 (0.32, 0.73)	0.50 (0.33, 0.76)
	Slope for winter min temp						-0.03 (-0.13, 0.06)		
	Slope for days of snow cover						-0.003 (-0.016, 0.010)		
	Slope for spring temperature							0.13 (-0.08, 0.34)	

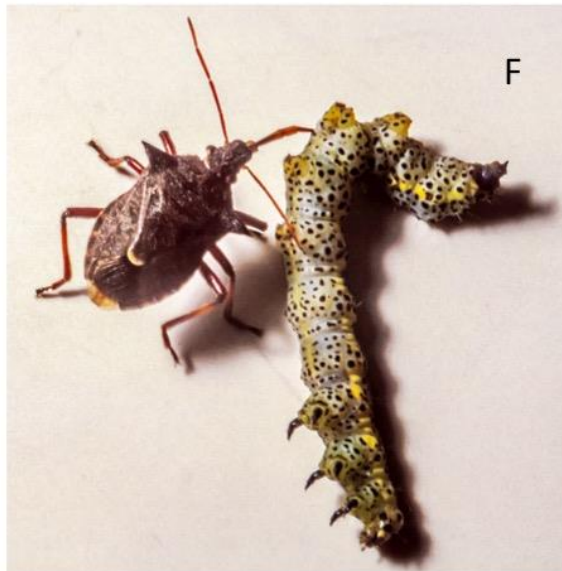
Slope for summer temp on larval survival									-0.04 (-0.17, 0.07)
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The first column show estimates for the base model that doesn't include environmental covariates, and where data are pooled across the four patches. The next four columns show estimates for the base model fitted separately to data from each patch. The next two columns show estimates for pooled data with additional covariates for the winter period from larvae to eggs. In the first of these, the covariates are winter minimum temperature and the number of days with snow cover. In the second, there is a covariate for spring temperature, which might affect the number of flying adults laying eggs. The last column shows results where development time in the egg-larvae model has been replaced with the average temperature over June and July.

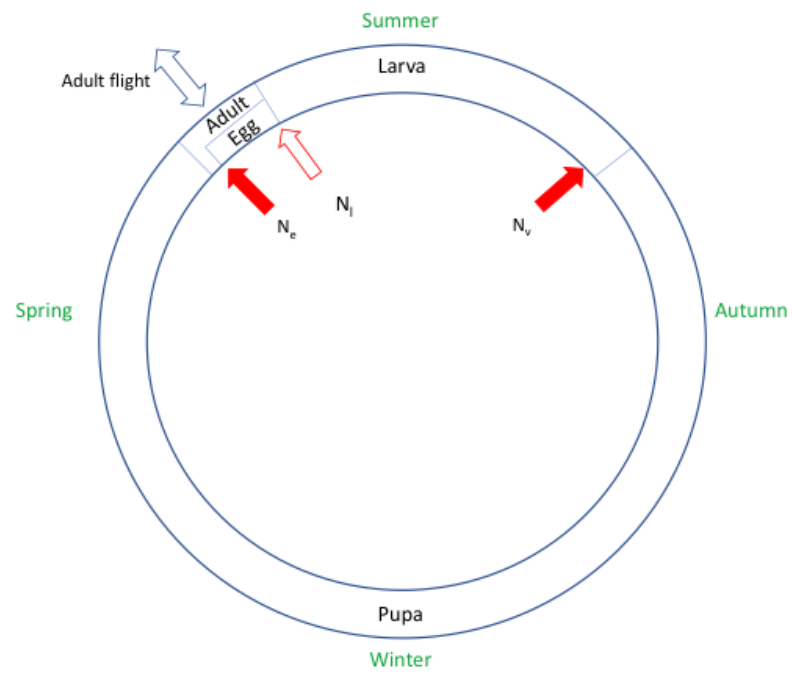
SKF Fig 1 (A-E)



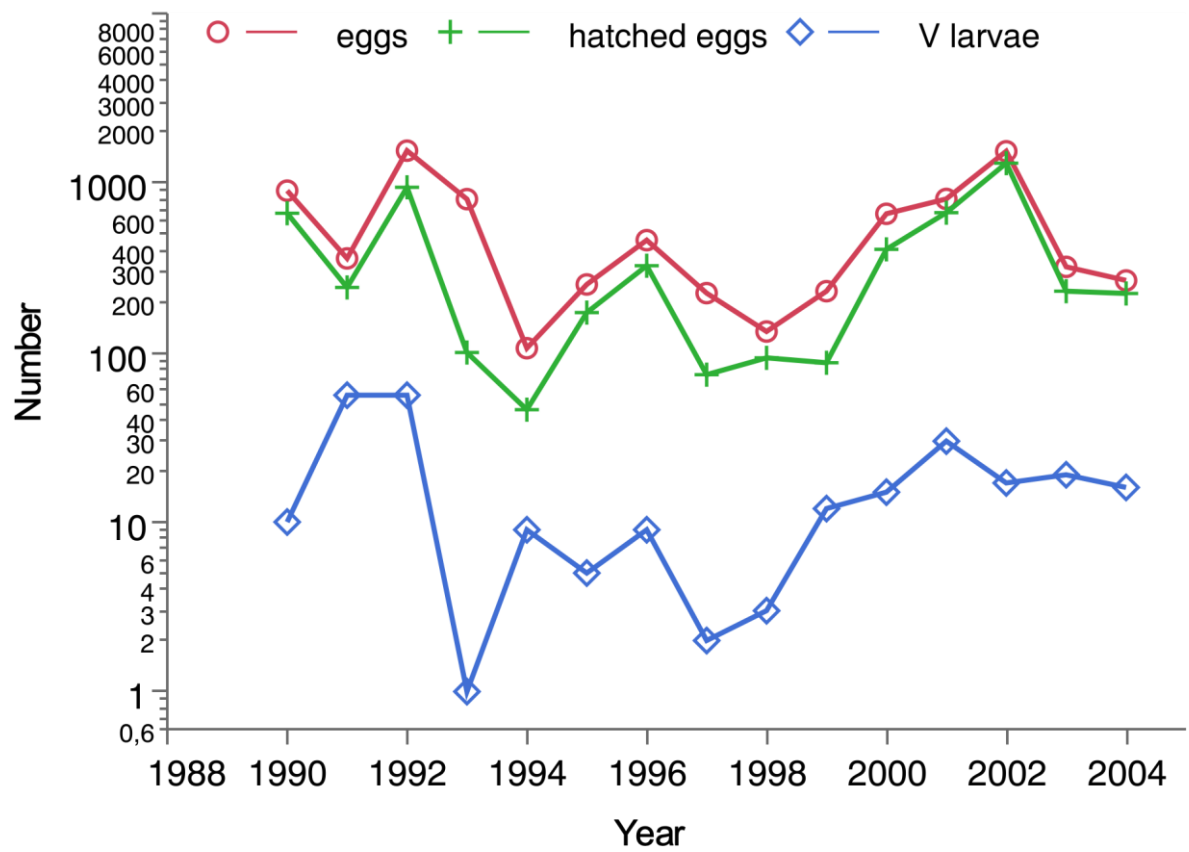
SKF Fig 1 (continued)



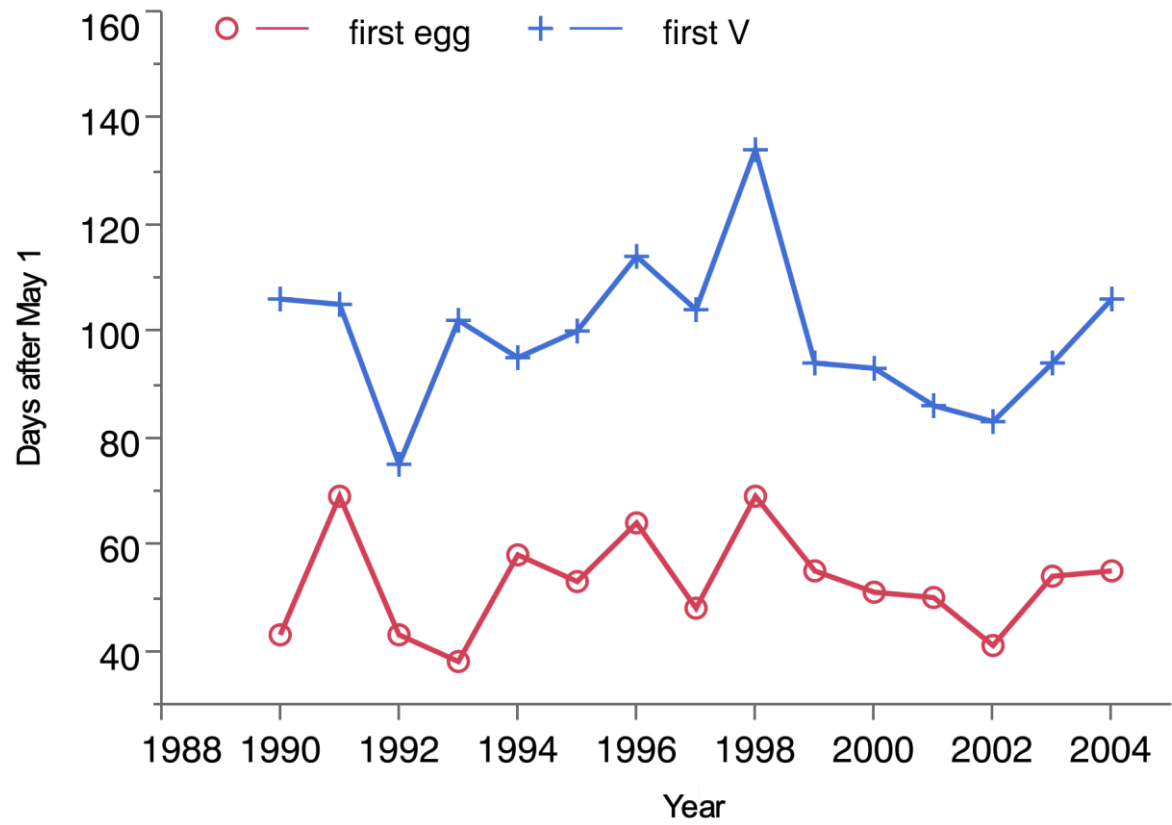
SKF Fig 2



SKF Fig 3

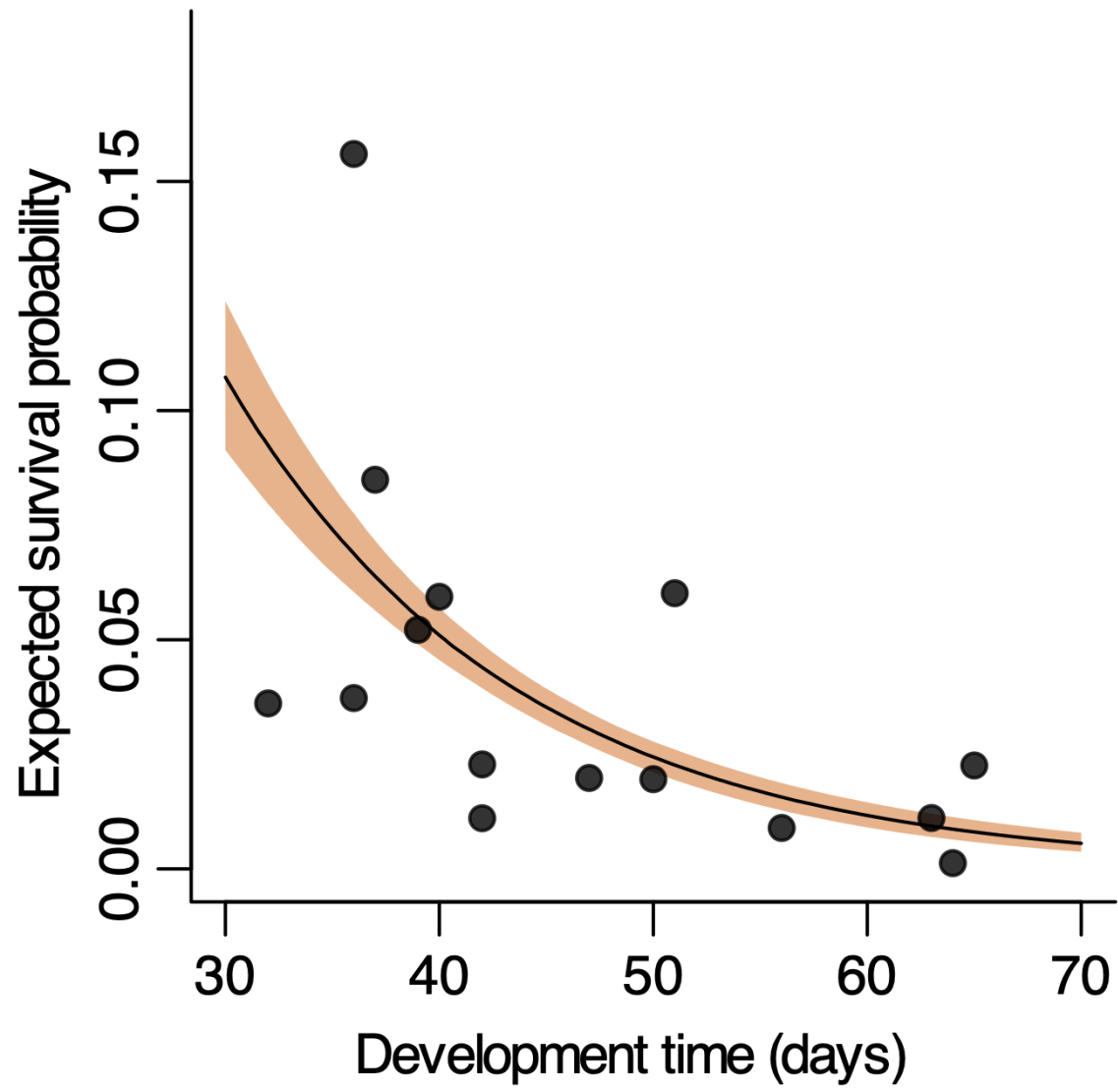


SKF Fig 4

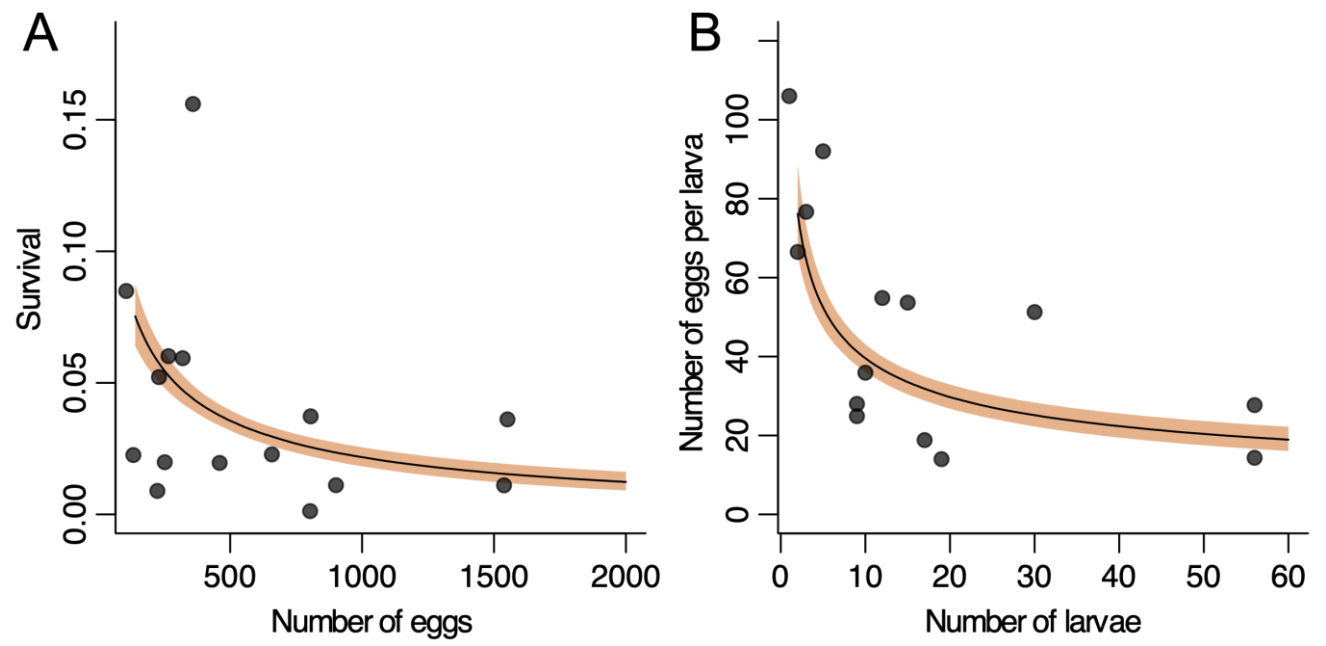




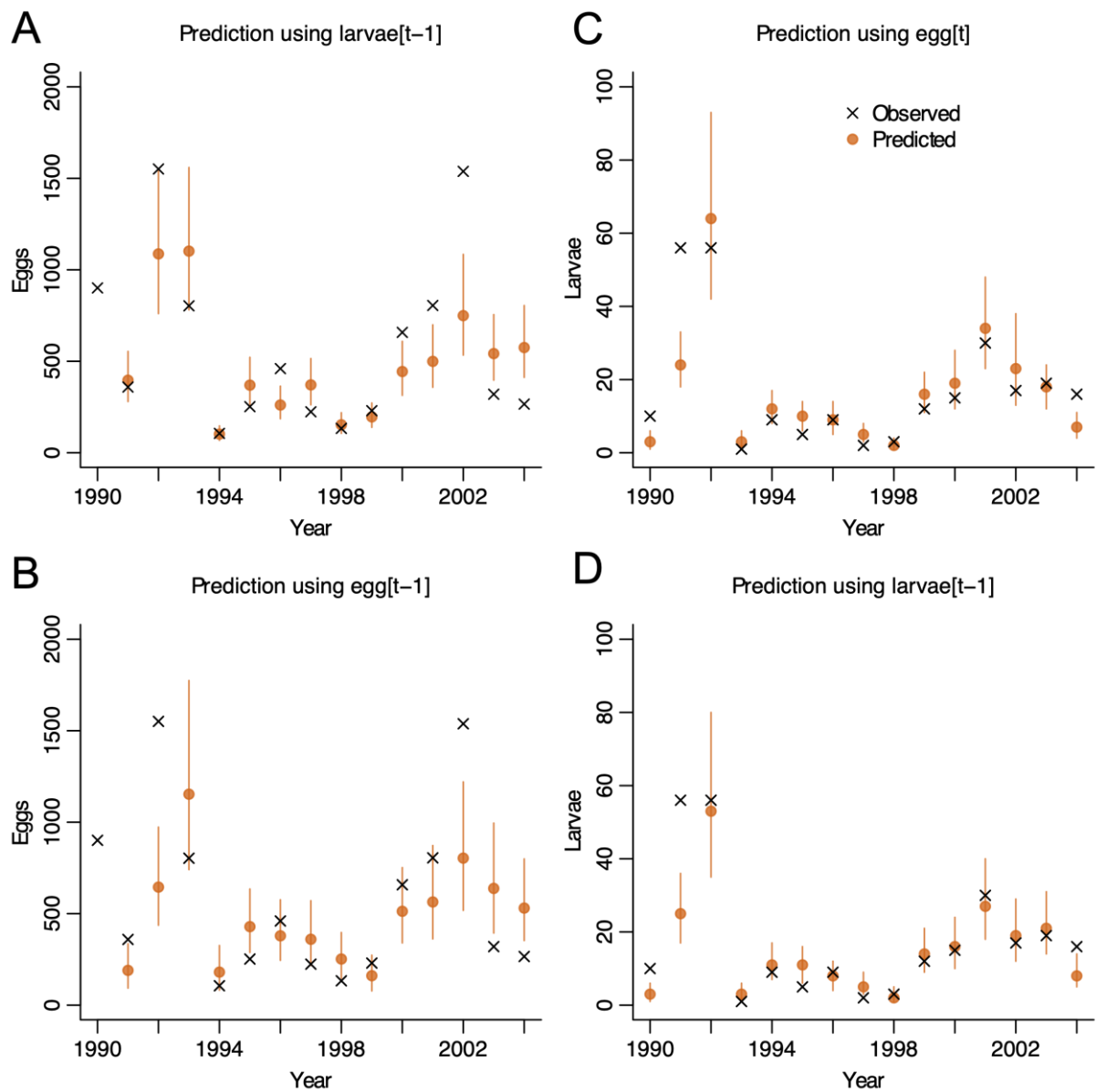
SKF Fig 5



SKF Fig 6



SKF Fig 7



SKF Fig 8

