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

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18 **Author contributions** CS and JF conceived the ideas, designed the work and collected the

19 data; JK and CS analyzed the data and wrote the paper; all authors approved the final version

20 for publication.

21

22 **Abstract**

23 Insect population dynamics are the result of an interplay between intraspecific competition,
24 trophic interactions and external forces such as weather conditions, but studying how these
25 processes combine to determine population change is challenging. We investigate
26 mechanisms of population dynamics in a natural, low density insect population. Eggs and
27 larvae of the noctuid moth, *Abrostola asclepiadis*, develop on its host plant during summer.
28 The population density, and mortality, was closely monitored throughout this period during
29 15 years. Densities fluctuated between one and two orders of magnitude. Egg – larval
30 developmental time varied substantially among years, with lower survival in cool summers
31 with slower development. This was presumably due to the prolonged exposure to a large guild
32 of polyphagous arthropod enemies. We also found a density dependent component during this
33 period, that could be a result of intraspecific competition for food among old larvae.
34 Dynamics during the long period from pupation in late summer through winter survival in the
35 ground to adult emergence and oviposition the next year displayed few clear patterns and
36 more unexplained variability, thus giving a more random appearance. The population hence
37 shows more unexplained or unpredictable variation during the long wintering period, but
38 seems more predictable over the summer egg-larval period. Our study illustrates how weather
39 - via a window of exposure to enemies and in combination with density-dependent processes -
40 can determine the course of population change through the insect life cycle.

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

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47 **Introduction**

48

49 Weather conditions are important factors in the dynamics of insect populations. Among the
50 various weather factors known to affect insects, temperature conditions are of particular
51 importance in temperate regions. Insects are ectotherms, and cool weather limits population
52 growth. Temperature *directly* affects many aspects of insect life such as growth rates, survival
53 probability, reproductive rates and flight propensity (Andrewartha and Birch 1954; Bale et al.
54 2002). In addition to these direct effects, weather conditions also impact insect populations
55 *indirectly* through the web of trophic interactions (Abarca and Spahn 2021). For example,
56 plant resources used by phytophagous insects are often affected by weather (DeLucia et al.
57 2012; Solbreck and Knape 2017; Hambäck 2021) thus impacting the food – herbivore link.
58 Interactions via the natural enemy link may also be modified by weather conditions (Barton
59 and Schmitz 2009; Barton and Ives 2014; Pepi et al. 2018)

60 Population dynamics are the result of this interplay between intraspecific processes,
61 trophic interactions and external forcing from weather conditions. Hence weather effects
62 should not be considered in isolation but in combination with other factors, particularly
63 density dependent trophic interactions (Varley et al. 1973; Royama 1992). The combined
64 effects of weather and web are often complex resulting in a wide range of dynamical
65 responses depending on the specific circumstances (Ives 1995; Stenseth et al. 2002; Walther
66 2010; Klapwijk et al. 2012; Lawson et al. 2015; Uszko et al. 2017). Due to these complexities
67 we still have a poor understanding how weather and future climates will affect insect
68 population change, motivating a continued analysis of specific population systems.

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

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

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

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

95

96

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

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

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

135

136 **Study area and host plant**

137

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

147

148 **Sampling**

149

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

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

164

165 **Weather factors**

166

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

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

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

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

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

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

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

199

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

201 We envisaged two possible weather factors that might affect overwinter survival of pupae: 1)

202 Winter minimum temperature. Very low temperatures could potentially cause freezing of

203 pupae. 2) The duration of the period with snow covered ground. This might, for example,

204 facilitate predation on pupae by winter active arthropod predators or small mammals. On the

205 other hand, snow cover acts as an insulation against cold and it could potentially shield pupae

206 from winter lows.

207 Both adult emergence and flight are likely affected by temperature. For example, high

208 temperatures are likely to provide more nights with good flight conditions resulting in more

209 eggs laid. In our analysis we used average May-June air temperature.

210 In summary the following factors were analyzed. For the egg – larva period (summer

211 period): Egg – larval development time was used as a token for air temperature. For the

212 overwintering period: Winter minimum temperature, number of days with snow cover and

213 mean air temperature for May-June. Standard meteorological data were obtained from

214 Stockholm, about 50 km to the north of the study area.

215

216 **Data treatment and population model**

217

218 We pooled data from the four patches because most of the individuals come from a single

219 patch, and the remaining patches had too few individuals to reliably fit our population model

220 below. For reference estimates from separate analyses of data from single patches are

221 however provided in Table 1. Insect abundance was measured at three points in the life cycle

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

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

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

233

234 ***Survival during egg – larval period***

235

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

238

$$239 \quad L_t \sim \text{Binomial}(E_t, s_t)$$

240

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

247 In terms of survival, the equation is

248

$$249 \quad s_t = \exp(- \exp(a + b \log E_t + c \log d_t + \varepsilon_t)) \quad \text{Eq 1}$$

250

251 where a is an intercept, b a slope for density dependence, d_t is the estimated development time

252 in year t and c its slope coefficient, and ε_t is a normally distributed random year effect. Under

253 this model, mortality increases and survival decreases as the coefficients increase. For

254 instance, a positive b would indicate negative density dependence. The choice of a

255 complementary log-log link and the inclusion of the logarithm of development time for

256 survival implies that the survival probability s_t corresponds to the survival probability up to

257 time d_t under a Weibull hazard rate (Pinder et al. 1998). This hazard is a power function of

258 time with shape determined by the parameter c (c=1 corresponds to a constant hazard) and

259 scale determined by the other covariates and the random effect.

260

261 *Pupal – adult survival to oviposition*

262

263 The second part of the model involves the process from [the latter part of] last instar larvae in

264 the autumn of year t to the number of eggs laid the following year. Thus, it may be seen as a

265 simple model of the combined effect of several subprocesses in the development from the

266 final larval stage, through the overwintering pupal and emerging adult stages. The per capita

267 productivity is modelled linearly on the log scale with an intercept term, a slope for the log

268 number of larvae describing density dependence, and a random year effect. To account for

269 demographic stochasticity in productivity we use Poisson distributions. The second submodel

270 therefore is

271

272 $E_t \sim \text{Poisson}(L_{t-1} \exp(\mu + f \log L_{t-1} + \eta_t))$ Eq 2

273

274 where μ is an intercept, f a slope for density effects and η_t is a random year effect.

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

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

285

286 **Results**

287

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

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

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

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

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

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

312

313 **Discussion**

314 **The dynamics of *A. asclepiadis***

315 A central question with regard to population change is to explore the mechanistic links
316 between population dynamics and climate variability (Stenseth et al. 2002; Boggs and Inouye
317 2012). We develop and analyze a model of the dynamics of a noctuid moth population based
318 upon long-term field data. The life cycle is divided into two phases (1) summer survival of
319 eggs and larvae, and (2) autumn – winter – spring survival followed by spring reproduction.
320 Our study suggests that summer weather effects are important. They seem to be mainly
321 indirect, operating via a window of vulnerability. Slower development of eggs and larvae at

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

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

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

341 There do not seem to be any important *direct* effects of temperature during the egg –
342 larval period. In rearing experiments encompassing a range of naturally encountered
343 temperatures there were no clear differences in egg or larval mortalities (Förare 1995a). There
344 are effects of temperature on pupal weight, but they are small for natural conditions (Förare
345 1995b). The dominating weather effect on *A. asclepiadis* populations during the summer
346 therefore seems to be the indirect effect on the window of vulnerability to enemies.

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

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

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

372 spring period with adult emergence, flight and oviposition.

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

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

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

389

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

391 What general conclusions concerning insect population dynamics in a new climate can be
392 drawn from our findings about *A. asclepiadis*? The population responses of insects to
393 weather/climate seem to harbour many idiosyncrasies. As mentioned, weather can influence
394 the dynamics of populations via multiple pathways, and can affect any stage in the life cycle
395 (e.g. Azerefegne et al 2001). They can act indirectly via the trophic web, and interact with
396 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**

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

429

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432

433 **Author contributions** CS and JF conceived the ideas, designed the work and collected the
434 data; JK and CS analyzed the data and wrote the paper; all authors approved the final version
435 for publication.

436

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438

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440

441 **References**

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556

557 **Figure legends**

558

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

566

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

574

575 Fig. 3. The numbers of eggs laid, eggs hatched and last instar larvae of *A. asclepiadis* 1990 –
576 2004.

577

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

579

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

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

583

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

587

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

593

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

600

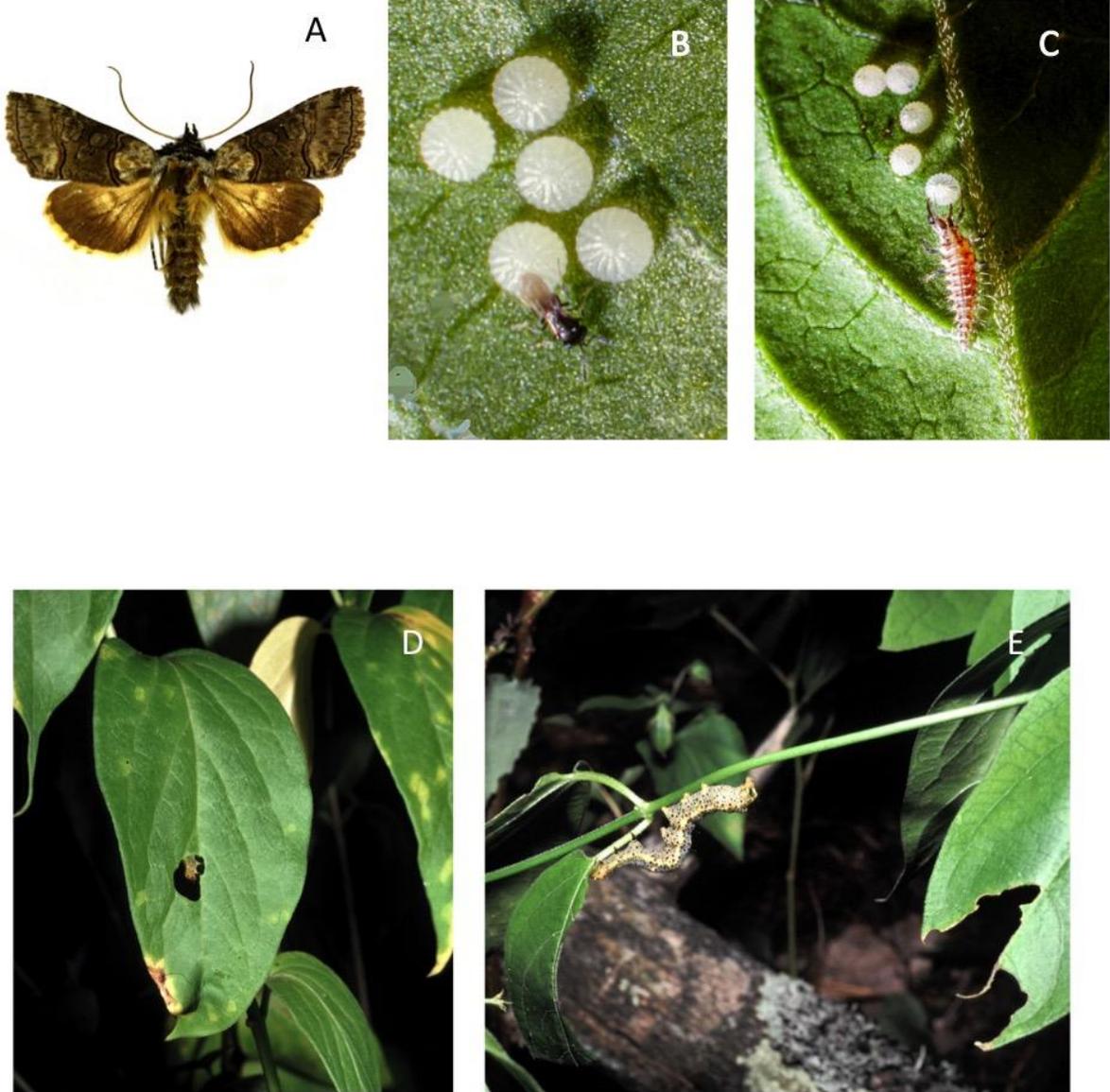
Table 1. Parameter estimates of the models.

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)	
σ_ε	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)
μ	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)
σ_η	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)	

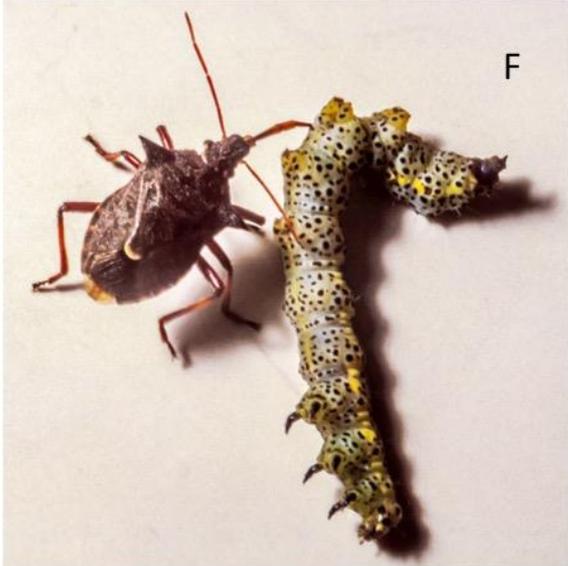
Slope for summer temp on larval survival									-0.04 (-0.17, 0.07)
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The first column show estimates for the base model that doesn't include environmental covariates, and where data are pooled across the four patches. The next four columns show estimates 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.

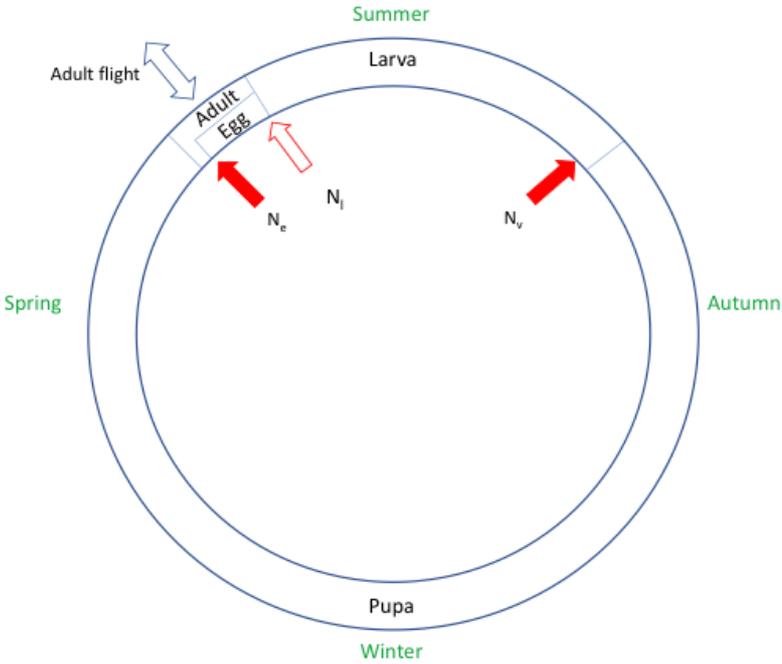
SKF Fig 1 (A-E)



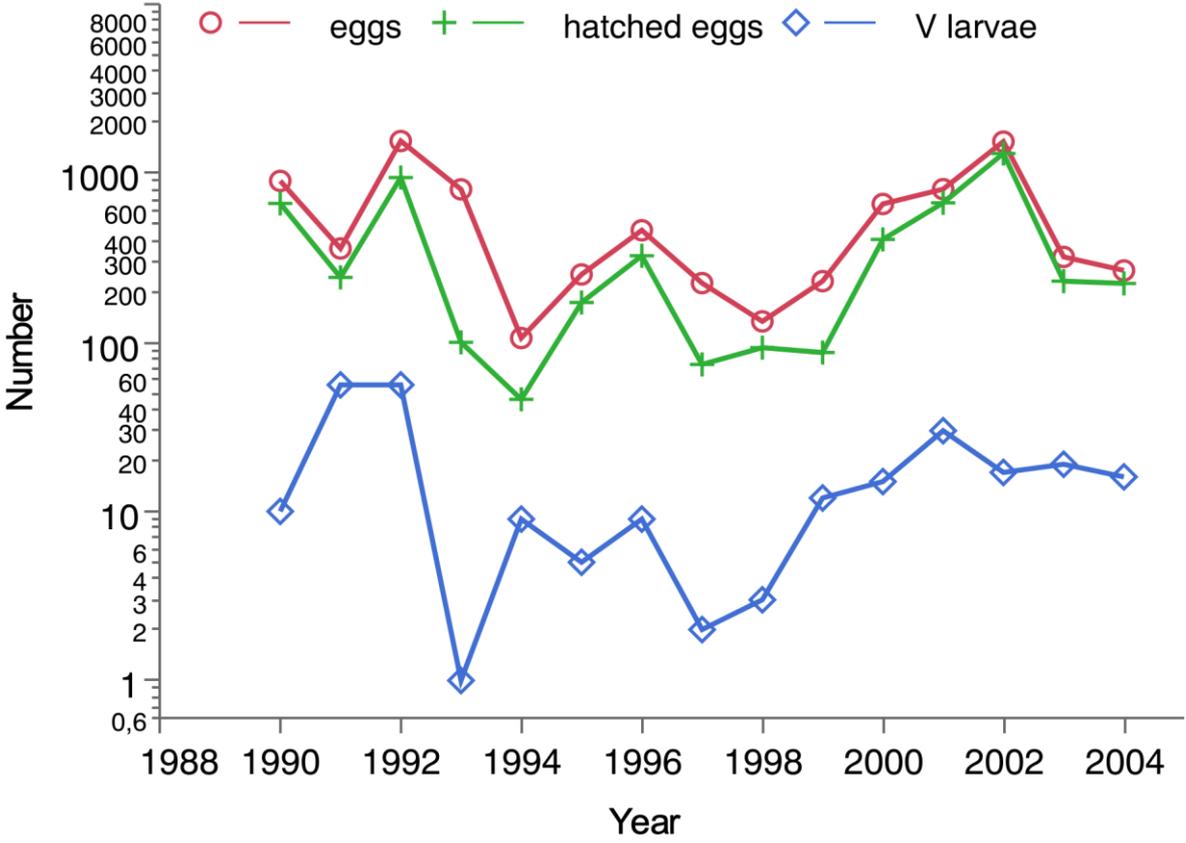
SKF Fig 1 (continued)



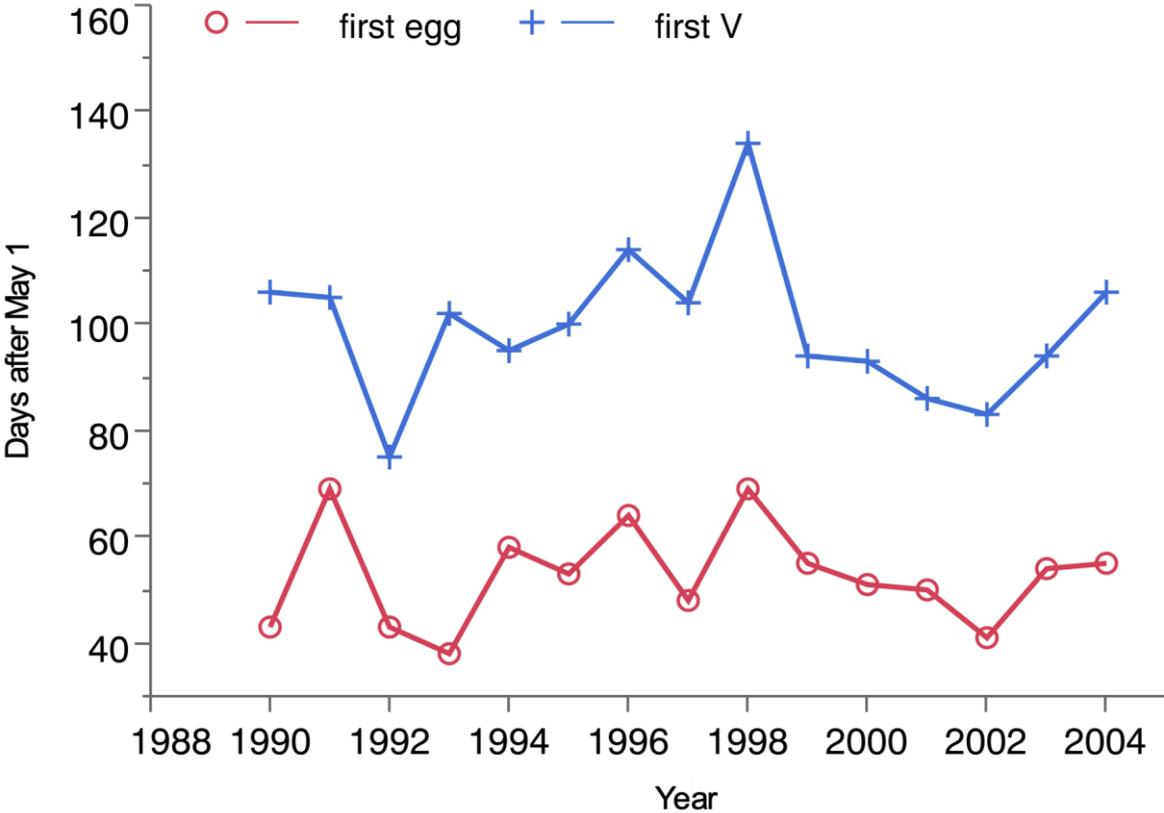
SKF Fig 2



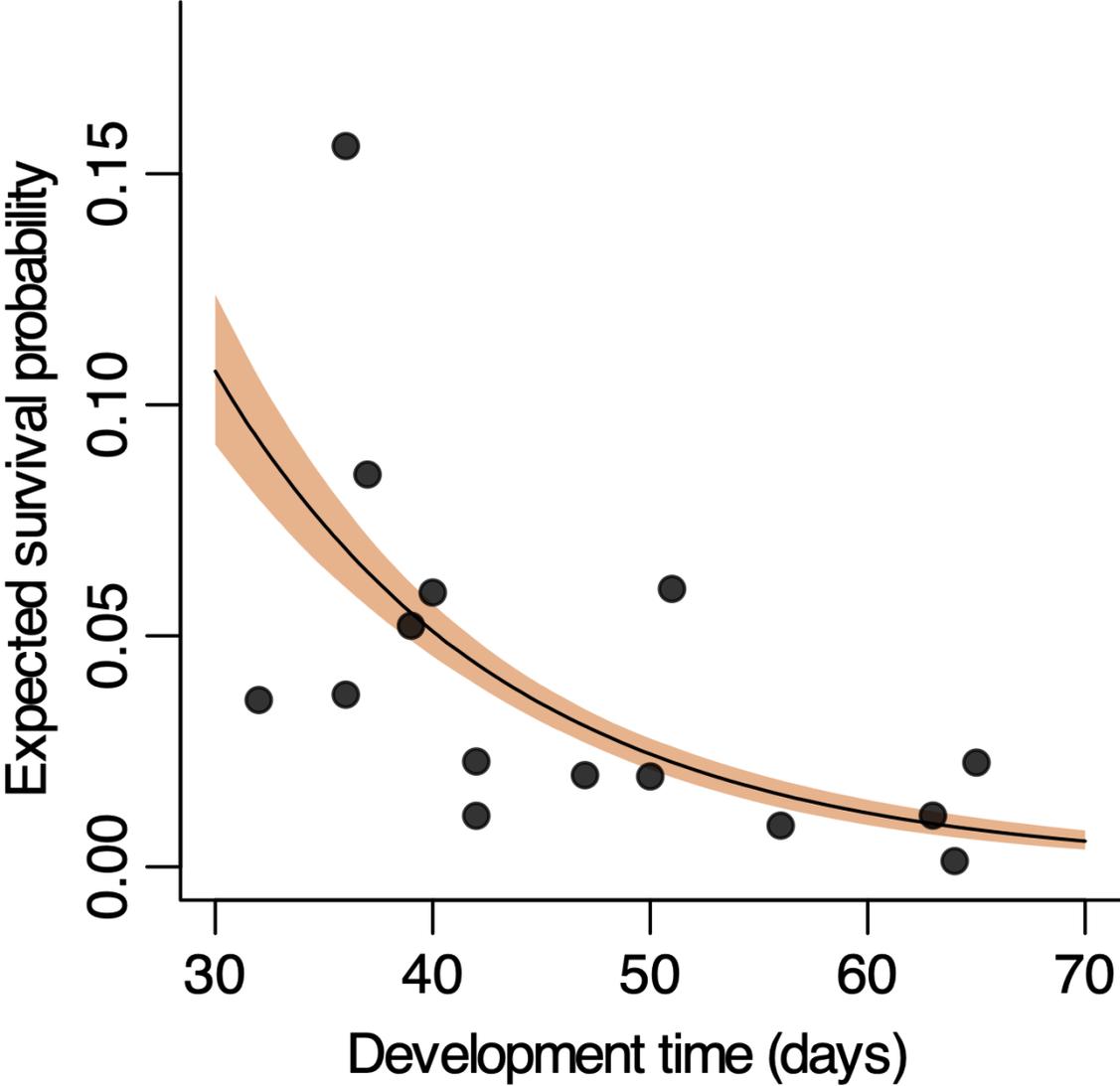
SKF Fig 3



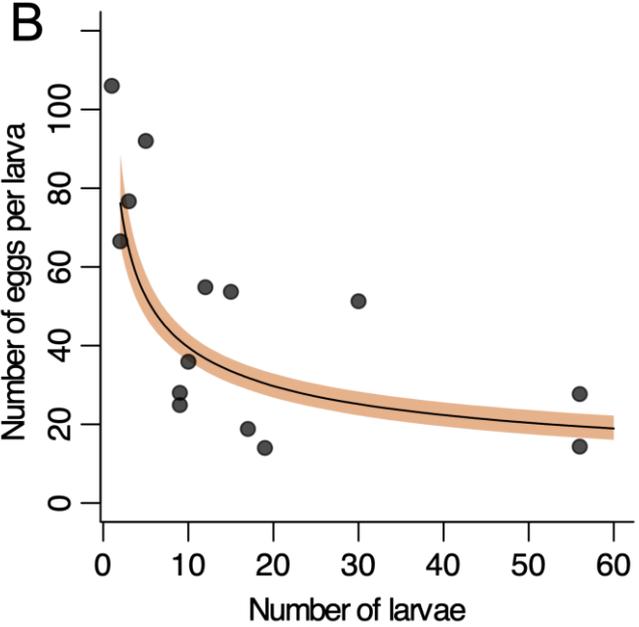
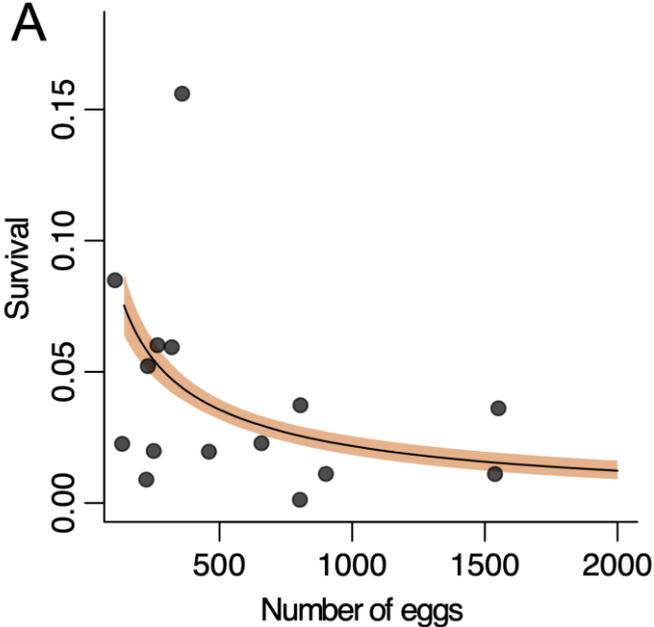
SKF Fig 4



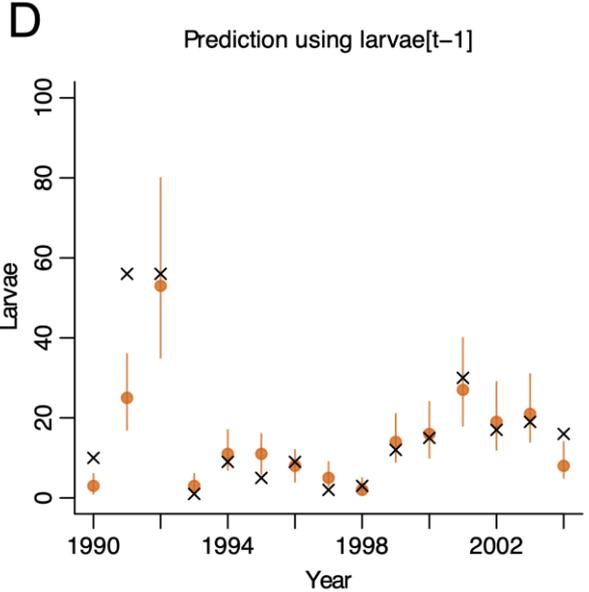
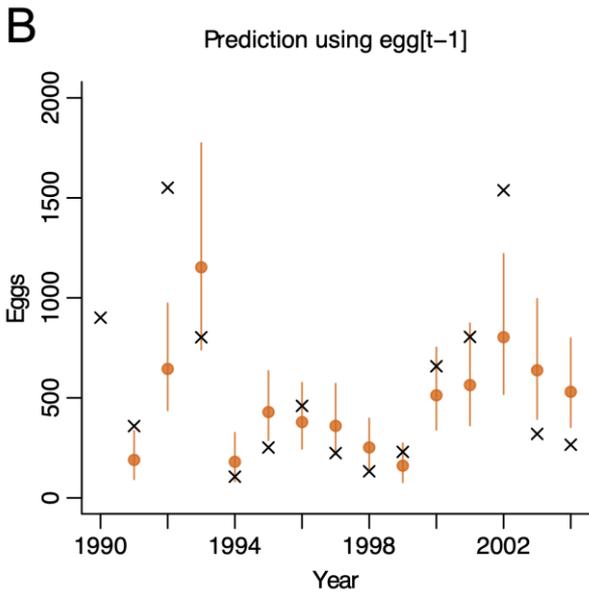
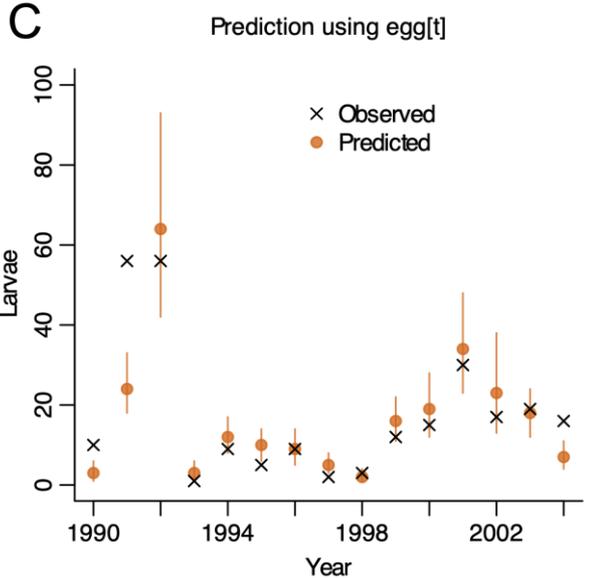
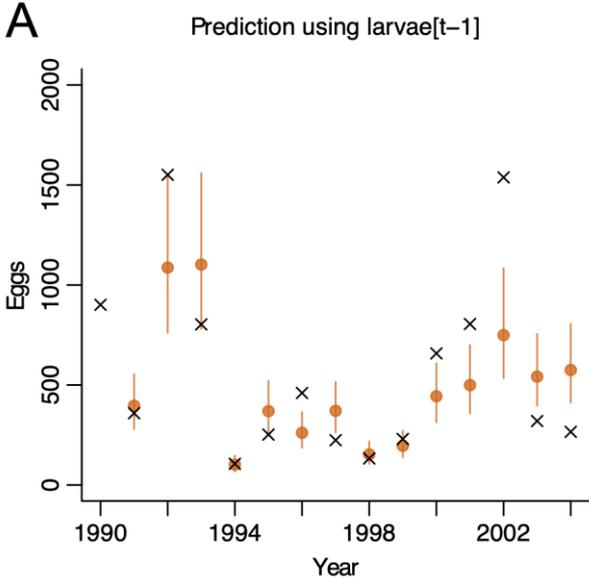
SKF Fig 5



SKF Fig 6



SKF Fig 7



SKF Fig 8

