Coping with shorter days: Do phenology shifts constrain aphid fitness?

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Abstract

1   Climate change can alter the phenology of organisms. It may thus lead seasonal organisms to face different

2   day lengths than in the past, and the fitness consequences of these changes are as yet unclear.

3   To study such effects we used the pea aphid *Acyrthosiphon pisum* as model organism as it has obligately

4   asexual clones, which can be used to study day length effects without eliciting a seasonal response. We recorded

5   life-history traits under short and long days both with two realistic temperature cycles with means differing by 2°C.

6   In addition we measured the population growth of aphids on their host plant *Pisum sativum*.

7   We show that short days reduce fecundity and the length of the reproductive period of aphids. Nevertheless

8   this does not translate to differences at the population level, because the observed fitness costs only become apparent

9   late in the individual's life. As expected, warm temperature shortens the development time by 0.7 days/°C, leading

10   to faster generation times. We found no interaction of temperature and day length. We conclude that day length

11   changes cause only relatively mild costs, which may not decelerate the increase in pest status due to climate change.

Introduction

13   Nearly all organisms need to cope with environmental heterogeneity and fluctuation;

14   showing a plastic response in the face of such heterogeneity can be beneficial. For example,

15   several species from the *Daphnia* complex (Cladocera) can grow a 'crown of thorns' in response

16   to predator pressure (Petrusek et al. 2009), and *Daphnia magna* allocates variable amounts of

17   energy to size and shape as adaptive induced response to predator presence (Rabus & Laforsch

18   2011). Similarly, many plants increase their investment into defence when attacked by

19   herbivores (e.g. Agrawal 2011). These examples demonstrate how phenotypic plasticity can

20   affect fitness. One of the most important fitness traits is phenology (Chuine 2010; Helm et al.

21   2013), i.e., the timing of life cycle events. Plasticity in phenology can profoundly change the

22   ecology of a species, as it can alter the timing of critical life-history events and synchrony with

23   other trophic levels (Visser et al. 1998; Visser & Holleman 2001). Thus phenological plasticity is

24   an important component of the ecology and evolution of species.

25   Phenotypic plasticity can not only be adaptive in temporally fluctuating environments,

26   but also prevent extinction in environments under directional change (Chevin et al. 2013). The

27   current rate of environmental change is likely unprecedented since 1400 years (IPCC WG I

28   2013), as the global surface temperature rises by 0.2°C per decade (Hansen et al. 2006). Climate

29   change modifies the onset and duration of seasons (Räisänen & Eklund 2012), and many species

30   have already responded by shifting their phenology in the according direction (Rosenzweig et al.

31   2007). By adjusting phenology *via* plastic responses, organisms can possibly mitigate the

32   extinction risk imposed by climate change (Charmantier et al. 2008; Vedder et al. 2013), and

33   even profit from it (Bell et al. 2015).

34   However, the evolution of phenotypic plasticity may be constrained by costs and limits

35   (DeWitt et al. 1998). For example, plasticity can be limited by tightly interacting species, which

36   may not shift their timing in synchrony. Among the best studied examples are great tit

37   populations which have lost synchrony with their caterpillar prey (Visser et al. 1998), and winter

38   moths which are no longer synchronous with their host (Visser & Holleman 2001). We

39   hypothesize that another limit of plasticity is posed by the reduction in day length (photoperiod)

40   associated with a shift in phenology: First, activities of a diurnal species, e.g. foraging, can be

41   constrained by shorter days, if individuals live in a later time of the year. Secondly, photoperiod

42   is the most common cue to predict seasonal change (Saunders 2013). Photoperiodism is

43   commonly assumed to be based on the circadian clock (Bünning 1936; Saunders 2013), a

44   molecular clockwork which governs rhythmicity (Peschel & Helfrich-Förster 2011). Thus we

45   hypothesize that altered day length conditions interfere with the (yet unresolved) interplay of

46   seasonal and circadian rhythmicity and hence affect phenotypic plasticity.

47   The effect of warming temperature on fitness is relatively well established. Within

48   physiological limits warmer temperature generally speeds up metabolic rates (Gillooly et al.

49   2001). Less researched, and potentially important in a changing climate, are interactions of day

50   length and temperature. We propose that warmer temperature results in faster growth during the

51   organism's active period, but higher energy expenditure during resting time. Hence, the effect of

52   temperature should depend on day length. Also, temperature might enhance the interference with

53   circadian timing, as the clockwork is not fully compensated for temperature changes (Saunders

54   2014). Thus, short day conditions may decrease insect fitness, whereas warm temperature should

55   enhance growth rates, and warming might enhance the fitness costs of short days.

56   Aphids like *Acyrthosiphon pisum* (HARRIS) are well suited to study constraints of short

57   days. During summer *A. pisum* reproduces clonally, establishing exponentially growing

58   populations. Live-born nymphs have, however, little chance to survive sub-zero temperatures

59   (Simon et al. 2002). Therefore, in many clones aphids give birth to a single generation of sexual

60   morphs in autumn, which produce cold-resistant eggs to overwinter. In warmer climates this

61   response to photoperiod is frequently lost, so asexual aphid morphs are active throughout the

62   year (Simon et al. 2002). These differences in phenology within one species allow studying day

63   length effects in a seasonal insect without actually inducing a photoperiodic response.

64   Specifically we hypothesize, that

65   (1) Shorter day length constrains aphid performance and reduces population growth.

66   (2) Warm temperature causes quicker generation cycles and faster population growth.

67   (3) Temperature and day length interact, so that the positive effects of an increase in

68   ambient temperature decline with shorter day length.

69   We therefore expect fitness costs under short-day conditions compared with long-day conditions,

70   and possibly the lowest fitness under short days combined with warm conditions.

71

Materials and Methods

73   To test for constraints of phenotypic plasticity, we carried out experiments with an

74   asexual clone of the aphid *A. pisum* in four climate chambers at the individual as well as at the

75   population level. We measured population growth on whole plants of *Pisum sativum* (L.), and

76   life history data of individuals raised on cut leaves of *P. sativum*.

77

78   Day length and temperature settings

79   We used four identical climate chambers (Sanyo/Panasonic MLR-H series), in which we

80   applied two realistic temperature settings with sinusoid day/night cycles, ranging from 12-23°C

81   (±1°C) and from 14-25°C (±1°C), and two day length regimes with day length of 12:12 LD and

82   16:8 LD (Fig. 1), using 40W fluorescent lamps. The temperature differed between the light

83   treatments at dawn and dusk, but this difference in light sums is only 1.2 %. Treatments were

84   exchanged weekly, because the maximum light intensities varied between chambers from 13,000

85   – 21,000 lux. Because development and reproductive period lasted four weeks, all treatments

86   received the same light sum [lux * h] over this period. The lower temperature settings in the

87   experiment approximately reflect naturally occurring temperatures in Würzburg, southern

88   Germany, during summer solstice (12-22°C) and during beginning of September (11-22°C; data

89   from Deutscher Wetterdienst, http://www.dwd.de/). The higher temperature settings simulate

90   climate change with moderately increased mean temperature of 2°C, which ranges between the

91   SRES B1 and B2 marker scenario projections for 2099 (IPCC WGIII 2000). We are aware that

92   this is a conservative estimate; we nevertheless used this low difference of means, so that we did

93   not confound the results by exceeding the physiological optimum of the pea aphid.

94

95   Study organisms

96   Due to its fast population growth and its properties as virus vector, *Acyrthosiphon pisum*

97   (HARRIS, Aphididae) is a pest in agriculture, which is distributed throughout northern Europe,

98   North America and New Zealand (Blackman & Eastop 2000). *Acyrthosiphon pisum* feeds on

99   legume crops such as pea (*Pisum sativum L.*) and bean (*Vicia faba L.*), and does not switch hosts

100   in autumn. The aphid clone L1_22, an asexual green alfalfa biotype, was kindly provided by Grit

101   Kunert (MPI Jena). The known asexuality of the clone has been confirmed by providing an 8:16

102   LD rhythm at 10°C for four generations.

103   *Pisum sativum* L. is a suitable host plant for *A. pisum*, and agricultural plants are frequently

104   attacked by aphids (Blackman & Eastop 2000). We used the breed 'Kleine Rheinländerin'

105   (Bingenheimer Saatgut, Echzell, Germany), which grows to 40 cm, for all experiments.

106

107   Performance of individual aphids

108   To detect day length and temperature effects on the individual performance of aphids, we

109   placed 20 adult apterous, asexual aphids per climate chamber (20 x 4 = 80) singly in plastic tubes

110   (8 x 3.5 cm), and used their first born nymphs (termed first generation) as new focal individuals

111   for further measurement. These first-generation nymphs were fed every second day with one cut

112   leaf each, and we recorded development time, length of reproductive period, post-reproductive

113   period and life span. We used cut leaves like Meister et al. (2006) to exclude differences in food

114   quality, as a living host plant can be expected to fix more carbon under long day conditions. We

115   counted and discarded newly born nymphs daily (thus measuring daily fecundity and lifetime

116   reproductive output of each focal animal). In order to test for maternal effects in a second

117   generation and to confirm the loss of sexuality in the clone we retained one early-born nymph

118   per focal aphid after 11-13 days. Additionally, we retained one late-born nymph after 29-31

119   days, because we expected the maternal effects to intensify as the adult ages. We raised all

120   aphids of the second generation under the same conditions (16:8 LD, 22°C and 60% humidity),

121   so that maternal effects could be distinguished from direct effects of day length and temperature.

122   These second generation aphids were fed with fresh plant material every second day, and life

123   history parameters were also recorded every second day.

124   To supply the aphid individuals with food we grew 60 pea plants ('Kleine

125   Rheinländerin') per week with two plants per pot (11x11 cm, filled with Einheitserde® classic

126   soil, Einheitserdewerk Hameln GmbH, Sinntal, Germany) over six weeks at 22°C, 16:8 LD and

127   60% humidity, so that 2-3 week old plant material (approximate BBCH growth stage 14-15) was

128   available over the whole course of the experiment. Pea plants grow pinnate compound leaves

129   with morphologically different stipules. We fed four leaflets from the same leaf compound (the

130   youngest which had completely unfolded leaflets), but excluded the basal stipulate leaves. If

131   there was not enough plant material available, we fed the aphids with plant material of two leaf

132   compounds of similar age. The four leaflets were randomly distributed over the four treatments

133   to ensure that all treatments received the same plant quality. We used the same plant no more

134   than twice in order to avoid induction of defense. The plants were always raised at 22°C and in a

135   16:8 LD cycle.

136   Altogether 80 individuals of the aphid *A. pisum* were used in the experiment. Nine aphids

137   died before reaching reproductive age, and six individuals (7.5%; five under cold, short day and

138   one under warm, short day treatment) developed into alate (winged) virginoparous morphs. The

139   15 deceased or winged individuals were excluded from further analysis. A further ten aphid

140   individuals were accidentally killed as adults, which reduced the number of replicates to 55

141   aphids for the traits fecundity, reproductive period, post-reproductive period and life span.

142

143   Population experiment

144   To detect the effects of day length and temperature on population demography, we sowed

145   60 pea plants into 11x11cm square pots filled with a peat-based substrate (Einheitserde® classic,

146   Einheitserdewerk Hameln GmbH, Sinntal, Germany). The plants were watered from above

147   during the first week and from below (using felt mats) thereafter in four trays with 15 plants

148   each. We kept all plants in a walk-in climate chamber with 22°C at 16:8 LD and 60% humidity

149   and watered five times per week. After 18 days we fixed each plant with raffia fibres to 50 cm

150   wood sticks. After 25 days 12 plants from each tray were evenly distributed over the four climate

151   regimes (48 plants in total), and the position within each chamber fully randomized. Following

152   one week of acclimation we established aphid populations by placing 10 individuals of adult

153   apterous (wingless) asexual morphs on each individually bagged plant, using micro-perforated

154   plastic bags (255x700 mm, 0.5 mm perforations, Baumann Saatzuchtbedarf, www.baumann-

155   saatzuchtbedarf.de). To accommodate for climate chamber differences we exchanged treatments

156   between chambers weekly. We estimated population size weekly by counts of alate (winged) and

157   apterous adults and nymphs (judged by the visibility of the cauda and size differences) over the

158   course of four weeks on the living plants (BBCH growth stages approximately 16-19). To

159   control the effect of heat stress on the plants we distributed 24 aphid-free, 23 days old plants over

160   the four chambers to observe plant responses to the artificial climate over four weeks.

161

162   Statistics

163   We used R version 2.15.2 (R Core Team 2012) for all analyses. On the individual level,

164   65 out of 80 aphids were used to assess development time, and 55 for the remaining variables

165   (length of reproductive period, length of post-reproductive period, life span and fecundity). We

166   tested effects of day length, temperature and their interactions as main factors in two-way

167   ANOVAs on all of those parameters except fecundity. The latter we used to construct a Leslie

168   Matrix to yield the theoretical population rate of increase r_t and the reproductive values of each

169   age cohort (Leslie 1945). We used a Leslie matrix, because averaged daily fecundity (as for

170   example used by Meister et al. 2006) does not account for skews in the fecundity curve, which

171   cause shorter generation times and alter growth rate projections. In particular, late-born offspring

172   add very little to population growth compared to early-born offspring, and the true fitness costs

173   may be over- or underestimated. We used the estimates of r_t in a two-way ANOVA to also test

174   for effects of day length and temperature. At the population level, we calculated the weekly

175   population growth rates r_1, r_2 and r_3 on 48 plants, as (N_x/N_{x-1}), using the aphid number N at week

176   x, and the daily growth as $r_x^{\wedge}(^1/_7)$. We compared the rates of increase, i.e. log(growth rates), in

177   two-way ANOVAs as before. Because a temperature gradient existed within the climate

178   chambers, the position within chambers had a significant effect for nymphal development and r_t.

179   However, as the position effect was in the same direction as the effect of temperature and did not

180   qualitatively change the results, we omitted it from analysis.

181

182

183

184   **Results**

185   Life history traits of individual aphids

186   In our experiment aphids developed on average within 10.7±0.2 days and warm

187   temperature shortened the development time significantly (Fig. 2, Table 1, Table 2). The length

188   of the reproductive period (Fig. 2, Table 1) and the fecundity of aphids (Fig. 3, Table 1)

189   depended solely on day length. Aphids raised under short-day conditions reproduced about 3

190   days (14%) less, and produced 22% fewer nymphs (Table 2). The post-reproductive period

191   ranged from 5.0±0.6 (warm, long) to 9.8±1.3 (cold, short) days, and was elongated by a

192   reduction of day length and of temperature (Fig. 2). Overall, warm temperature shortened the

193   total life span, i.e. the sum of development time, reproductive and post-reproductive period. Even

194   though the food quality was sufficient for full development (including the post-reproductive

195   period) of all focal aphids in the first generation, the second generation suffered high mortality

196   rates (34%) and reduced offspring numbers (to 0-30%). 73 out of 75 surviving adults of the

197   second generation reproduced and no males were observed; so we confirm that the focal aphids

198   did not switch from asexual to sexual offspring. The theoretical population rates of increase r_t

199   (based on Leslie matrices) differed significantly between temperature regimes, but were

200   independent of day length (Fig. 4a). The reproductive values of the last three days of

201   reproduction were on average 1.56, which is 9.7% of the maximum reproductive value (16.99).

202   The average growth rate was below the growth rate of the population experiment (see next

203   section), possibly because the cut leaves do not provide enough phloem pressure.

204

205   Fitness costs on the population level

206   In the population experiment, about 10% of the observed aphids were adults, and 0% (in

207   the first two weeks) to 13% (in the third week) of the adults were winged. Adult/nymph ratios

208   and winged/wingless ratios never varied significantly among treatments (all p>0.1), so

209   differences in wing induction patterns are unlikely to have affected our results. Aphid density

210   (sum of nymphs, winged and wingless aphids) increased exponentially over the first two weeks,

211   with a weekly growth of about one order of magnitude (Fig. 4b). After two weeks aphid densities

212   were higher in the warm treatment (1027±101 aphids) than in the cold treatment (668±42

213   aphids), but not significantly affected by day length (Table 1). In week three the exponential

214   growth ceased, and during weeks three and four most plants died and aphid densities declined,

215   especially in the warmer treatments. Control plants without aphids did not show any signs of heat

216   stress and were healthy throughout the experiment.

217

218   **Discussion**

219   Plasticity in phenology likely helps to make use of novel climate conditions and to extend

220   the asexual season, which may increase the pest status of aphids (Bell et al. 2015). However, the

221   novel day length conditions under which the animals live may be non-optimal to the organism,

222   and thus reduce the advantage of plasticity. Our results show that a 2°C increase in temperature

223   accelerates development and increases the population growth in an asexual aphid clone, but does

224   not alter the individual reproductive period or fecundity. In contrast to increased temperature a

225   shorter day length reduced the length of the reproductive period by 14% and fecundity by 22%,

226   but did not significantly affect development time or life span.

227

228   Day Length

229   In our experiment day length alters fecundity and length of the reproductive period and

230   aphids suffer under short- day environments from reduced reproduction.

231   Even though variation in phenological traits is commonly regarded as phenotypic

232   plasticity (Charmantier et al. 2008; Vitasse et al. 2010; Vedder et al. 2013), the

233   microevolutionary costs and limits of plasticity (sensu DeWitt et al. 1998) in phenology have to

234   our knowledge never been measured. Phenotypic plasticity in phenology often relies on day

235   length (photoperiod) as cue, and our study is the first that demonstrates fitness costs linked to

236   short days in insects. On living plants aphids exhibit circadian rhythmicity and seem to be day-

237   active (Eisenbach & Mittler 1980; Hodgson & Lane 1981; Cortes et al. 2010), which offers – in

238   agreement with the hypothesis outlined in the introduction – a tentative explanation for the

239   observed fitness loss under short days. Further studies will need to verify the diurnality

240   independent of host plants, and to measure phloem consumption under long and short days.

241   Photoperiod may also have a less direct effect on fitness, as its measurement may be

242   based on the circadian clock (Bünning 1936), an endogenous time-keeping mechanism which

243   relies on two cyclically expressed protein complexes, PERIOD/TIMELESS and

244   CLOCK/CYCLE (Peschel & Helfrich-Förster 2011). Interference among seasonal rhythm and

245   circadian clock seems reasonable, though this hypothesis is still under debate (Danks 2005;

246   Kostal 2011). Hence shortening day length may not only affect the time available, but also its

247   correct measurement. So far, relatively little is known about the circadian rhythm of aphids, but

248   with the recent identification of the clock genes in aphids (Cortes et al. 2010), further progress

249   can be expected.

250   On the population level we did not detect effects of day length on fitness. Our calculation

251   based on Leslie matrices indicates that short day length does not significantly dampen population

252   growth, because the additional offspring produced under long days are born rather late in the

253   adults' life (c.f. Fig. 2); thus only life stages with little reproductive value are affected.

254   Consequently, substantial costs of shortened day length are not observed in our population

255   experiment. We thus conclude that the observed reduced reproduction does not impede

256   population growth.

257

258   Temperature

259   As expected, we found that warmer temperature shortens the life cycle of aphids. Because

260   the quicker life cycle leads to faster population growth both in our Leslie calculations and on real

261   plants, climate change with increased mean temperatures should increase the pest potential of

262   aphids (Bell et al. 2015). Presumably warmer temperature acts on metabolic rates, as is well

263   established for insects (Gillooly et al. 2001). Temperature did, however, not change fecundity or

264   the length of the reproductive period over the measured range, and thus warm temperature *per se*

265   does not affect an individual's condition. This contradicts studies of temperature on the condition

266   of A. *pisum* by Campbell & Mackauer (1977) and Kaakeh & Dutcher (1993), but supports the

267   results of Kilian & Nielson (1971). On a different aphid species, Rispe et al. (1996) also detected

268   no general effect of temperature on fecundity, but large variation among clones. Clonal variation

269   also explains differences between the cited experiments.

270   Because variability in temperature will likely increase due to climate change (Solomon et

271   al. 2007), we included diurnal cycles in our design. Due to the nonlinear shape of the growth rate

272   curve, variability should increase the growth rate as long as it is below the optimum (Estay et al.

273   2013). Several studies on other clones indicate that the physiological optimum of *A.pisum* lies

274   beyond 20°C, and decreases only at temperatures higher than 25°C to 30°C (Kenten 1955; Kilian

275   & Nielson 1971; Campbell & Mackauer 1977; Kaakeh & Dutcher 1993; Rispe et al. 1996). Our

276   treatments lie with 17.5 and 19.5°C below the reported optimum, so one would expect a larger

277   effect of an increase in mean temperature on reproductive traits in our experiment compared to

278   experiments applying constant temperatures. However, this hypothesis was not supported by our

279   experiment. Kilian & Nielson (1971) and Kaakeh and Dutcher (1993) recorded with constant

280   temperatures around similar means (15/20°C) a shortening of development time by 0.7 and 1.2

281   days/°C, respectively. These values are largely in line with those in our experiment, where the

282   onset of reproduction shifted by 0.7 days/°C. We found however some effect of temperature

283   variability on longevity, because in contrast to Kilian and Nielson (1971), in our study life span

284   decreased under long days by 1.4 days/°C. Possibly, our clone is adapted to colder temperature,

285   so that the maximum temperatures of 25°C stressed the aphids and caused a hazard. Therefore

286   higher temperature variability may decrease, not increase, aphid performance.

287
288   Contrary to our hypothesis that temperature has opposing effects at day and night, we

289   found no interaction of day length and temperature. We hence conclude that day- and night time

290   temperatures have similar effects on aphid fitness and impose physiological constraints only by

291   generally affecting the aphid metabolism.

292

293   **Conclusion**

294   We show that a shorter photoperiod reduces reproduction in obligately asexual aphids.

295   Consequently, the aphids' potential benefits following from global change are reduced, as

296   temperature increase may lead to novel day length-temperature correlations. If the fitness decline

297   has its roots in physiological constraints, our results may be extrapolated to any day-active insect

298   species. However, these side-effects of phenotypic plasticity were not detected at the population

299   level, because they affect only late fitness components in the individual's life. We further show

300   that warm temperatures increase aphid growth by shortening development, but neither reduce

301   individual reproduction, nor do they modulate the effect of short day length. Taken together, we

302   conclude that novel light : temperature relations do not suppress the pest potential of aphids in a

303   changing climate.

304

305

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ANOVA tables testing for day length and temperature effects on aphid life history traits. Significant effects are shown in bold.

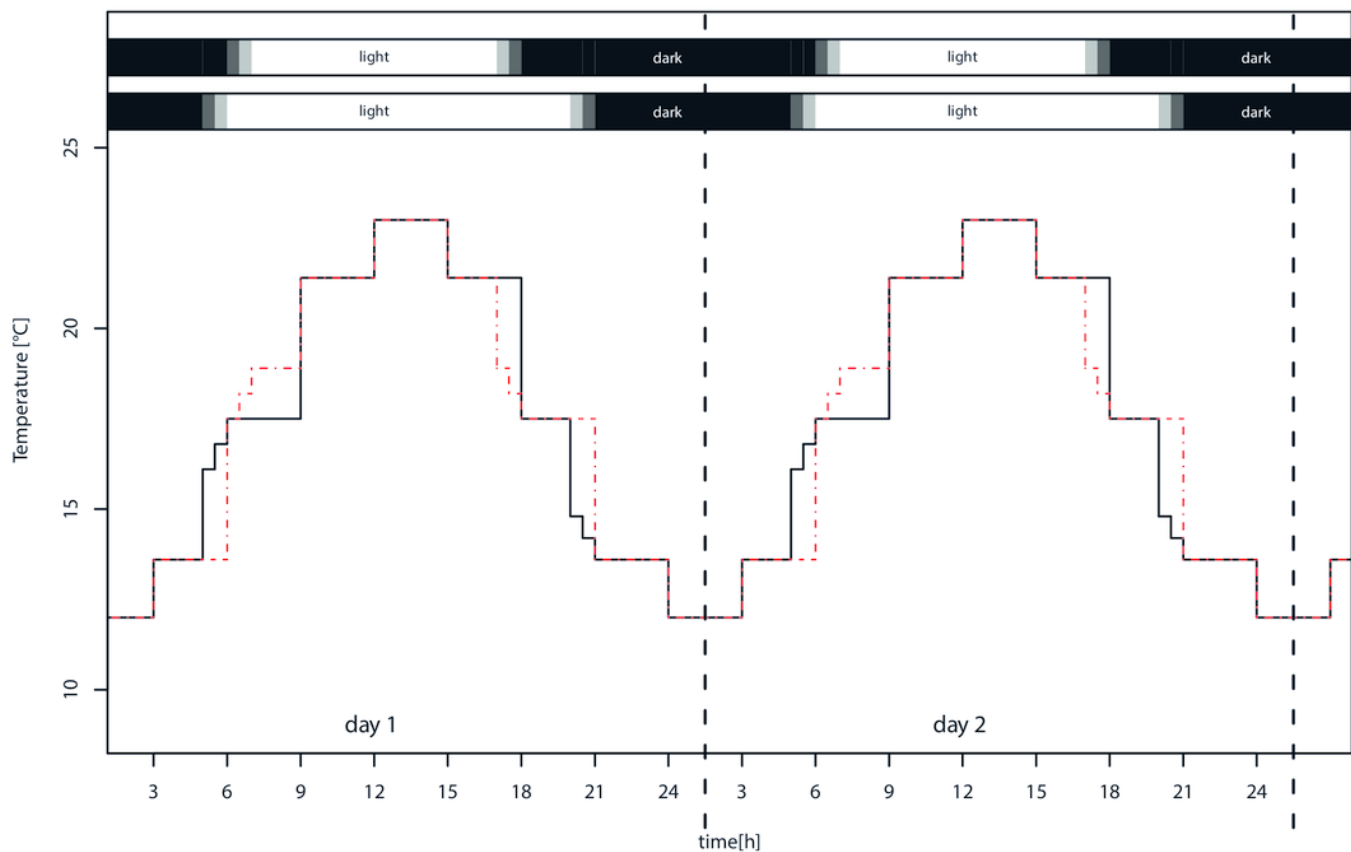
Response variable	Factor	F	df	p (<F)
Development time	Temperature	23.62	3,64	**<0.001**
	Day length	0.10	3,64	0.759
	Temp x day length	2.01	3,64	0.162
Reproductive period	Temperature	0.27	3,54	0.603
	Day length	6.98	3,54	**0.011**
	Temp x day length	0.22	3,54	0.643
Post-reproductive period	Temperature	6.36	3,54	**0.015**
	Day length	6.22	3,54	**0.016**
	Temp x day length	0.11	3,54	0.747
Life span	Temperature	9.24	3,54	**0.004**
	Day length	0.33	3,54	0.567
	Temp x day length	1.22	3,54	0.274
Total fecundity	Temperature	1.33	3,54	0.253
	Day length	12.84	3,54	**<0.001**
	Temp x day length	2.70	3,54	0.107
R_t (rate of increase derived from life-history traits)	Temperature	6.90	3,54	**0.011**
	Day length	0.08	3,54	0.773
	Temp x day length	2.95	3,54	0.092
Population rate of increase	Temperature	4.92	3,41	**0.032**
	Day length	0.04	3,41	0.836
	Temp x day length	0.54	3,41	0.465

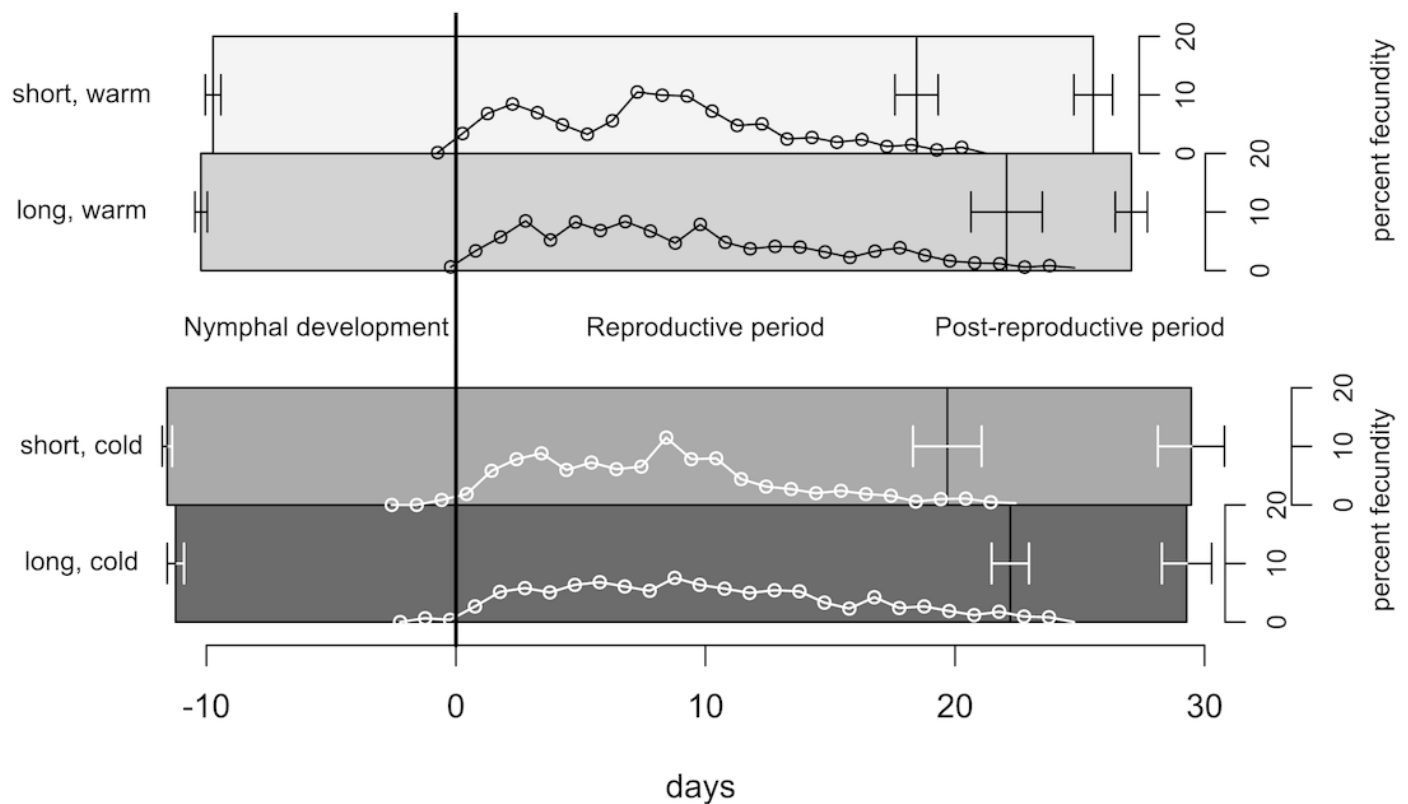
Effect sizes of the four day length/temperature treatments on aphid life history traits.

Response variable		Short day		Long day	
Development time [days]	Low temp	11.6	(±0.2)	11.2	(±0.3)
	High temp	9.7	(±0.3)	10.2	(±0.3)
Reproductive period [days]	Low temp	19.7	(±1.4)	22.2	(±0.8)
	High temp	18.5	(±0.9)	22.1	(±1.4)
Postreproductive period [days]	Low temp	9.8	(±1.3)	7.1	(±1.0)
	High temp	7.1	(±0.8)	5.0	(±0.6)
Life span [days]	Low temp	41.1	(±1.2)	40.3	(±1.4)
	High temp	35.0	(±1.1)	37.4	(±1.8)
Total fecundity [nymphs]	Low temp	54.2	(±4.7)	77.7	(±2.9)
	High temp	56.5	(±4.1)	65.3	(±5.5)
R_t (rate of increase derived from life- history traits)	Low temp	0.23	(±0.003)	0.24	(±0.004)
	High temp	0.26	(±0.009)	0.25	(±0.010)
Population rate of increase	Low temp	0.24	(±0.010)	0.25	(±0.017)
	High temp	0.31	(±0.012)	0.29	(±0.039)

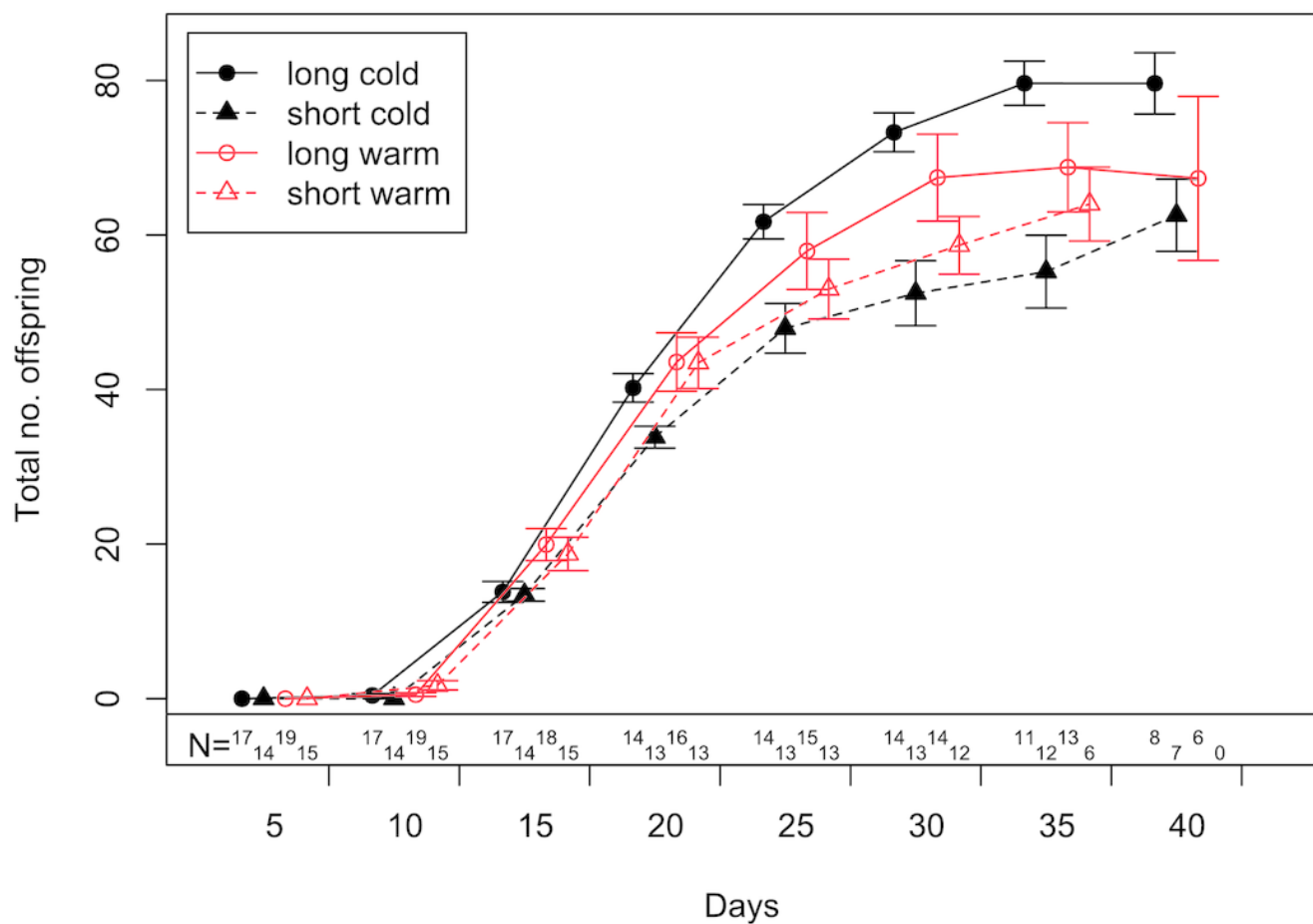
1

Temperature settings of the climate chambers

Warm temperature settings for long day (solid lines, lower bar) and short day (dashed lines, upper bar) treatments. Mean temperatures of long and short day conditions do not differ. The temperature in the two low temperature treatments was overall 2°C lower (not shown).

Life-history traits of individuals reared under different climate conditions.

The bars are aligned at the mean onset of reproduction (i.e. not left-aligned) to better distinguish temperature effects (on development) from day length effects (on reproduction). Bars indicate S.E. Lines with open circles indicate the timing of nymph production (expressed as daily contributions to total fecundity in %). These curves form also the basis for the Leslie calculations (Table1, Table 2). Statistics see Table 1.

3

Cumulative fecundity as function of age of individuals reared under four climate conditions.

Bars indicate S.E. Statistics see Table 1. Sample size (N) declines over time, because the aphid mortality increases with age (c.f. Fig. 2).

4

Growth rates of aphids under warm and cold conditions at 16:8h and 12:12h day length

A) Comparison of population rates of increase under warm vs. cold and under long day vs. short day conditions. Data is based on Leslie-matrices derived from individual life histories. Bars indicate S.E. B) Population growth of aphids reared on whole plants. Dashed lines indicate the time when half of the plants died, presumably from increasing pest load. Statistics see Table 1.