

Benefits and costs of aphid phenological bet-hedging strategies

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Reviewable

v1

Received: 16 Jun 2016 | Published: 17 Jun 2016

Citation: Joschinski J (2016) Benefits and costs of aphid phenological bet-hedging strategies. Research Ideas and Outcomes 2: e9580. doi: [10.3897/rio.2.e9580](https://doi.org/10.3897/rio.2.e9580)

Abstract

Intended readership

I am looking for a host institute to research bet-hedging strategies in the seasonal reproductive mode switches of aphids. The intended methods leave room for collaborative side-projects beyond the study question (e.g. molecular control of photoperiodism, or sharing aphid lines from throughout Europe), so this article might be of interest to anyone working with aphids. In addition, I would be happy to receive feedback from experts in bet-hedging theory, phenotypic plasticity and photoperiodism.

Summary

Global change causes both mean temperature and temperature variability to increase. Organisms can cope with predictable change in means, but increasing variability is less tractable. One strategy to increase survival chances in unpredictable environments is diversified bet-hedging, i.e. spreading the risk by variation in phenotype expression. Despite being considered a general mechanism, definite evidence for bet-hedging is scarce, as it requires both the demonstration that phenotypic variance correlates with environmental variability, and that it maximizes fitness.

When assessing fitness, one needs to account for both the benefits and costs of bet-hedging. Bet-hedgers produce suboptimal phenotypes in average years, resulting in decreased arithmetic mean fitness. But this temporary reduction is more than compensated

by elevated fitness in harsh years, so this well-known short-term fitness effect is not considered a real cost of bet-hedging. In contrast to the effects on arithmetic mean fitness, I hypothesize that bet-hedging also carries a long-term (geometric mean) fitness costs, in that the ability to generate phenotypic variance is costly *per se*.

With this research idea I seek evidence for bet-hedging and assess its costs and benefits, using aphids and their polyphenism in reproductive modes as model system. I plan to use aphid clones from environments along a gradient of temperature variability, and induce switches in reproductive modes under controlled conditions. To test for bet-hedging, I will correlate variance in phenotype determination with variability of the original environment. To determine the costs of bet-hedging, I will compare population growth of bet-hedgers with non-hedging clones. I will then combine benefits and costs of bet-hedging by calculating the geometric (long-term) mean fitness in predictable and unpredictable environments.

Keywords

bet-hedging; stochastic polyphenism; fluctuating natural selection; phenotypic plasticity; phenology; photoperiodism; circadian clocks; aphids; *Acyrtosiphon pisum*; *Rhopalosiphum padi*; *Megoura viciae*

Objectives, Concept and Approach

Climate change is the largest challenge of the 21st century (IPCC 2014). Temperatures will rise by at least 1.5 °C in the course of the next 100 years, and possibly even more important, extreme events will become more frequent (IPCC 2014). To some extent species can tolerate such change, but change beyond tolerable limits leads to species extinctions (Urban 2015).

When climate change drives environmental parameters out of tolerable limits, survival is generally considered to depend on microevolution and phenotypic plasticity (Charmantier et al. 2008, Chevin et al. 2010, Karell et al. 2011, Vedder et al. 2013). Microevolution of reaction norms and phenotypic plasticity are however of limited use in an unpredictable environment (Tufto 2015). Phenotypic plasticity relies on the prediction of future conditions, for example day length changes in autumn predict the occurrence of frost in winter. Because climate variability alters the covariance structure of environmental parameters (Jackson et al. 2009), cues that used to predict environmental hazards become less reliable. Thus, other strategies are needed.

Bet-hedging is adaptive variance of phenotypes around an 'optimal' mean value that can buffer against unforeseen environments. For example, variability in seed germination ensures that not all seeds enter the vulnerable seedling stage at the same time, so dormant seeds can survive to the next year under adverse conditions (Cohen 1966). Despite its relevance for coping with climate change, definite evidence for bet-hedging is scarce (Simons 2011): While many studies demonstrate environmental variability or

phenotypic variance, or a correlation of both, only few show that the variance has fitness consequences. Fewer still assess the geometric mean fitness and show that bet-hedging is advantageous on the long term. An ideal test of bet-hedging would provide a quantitative fit of the degree of bet-hedging with environmental variance (category VI evidence in Simons 2011), but only four studies (three plant species, one copepod) provide such strong evidence. Hence, to demonstrate the ubiquity and diversity of bet-hedging strategies, more studies on under-represented taxa are needed.

Costs and limits of bet-hedging

Why is evidence for bet-hedging so scarce? On the one hand, the prevalence of bet-hedging might be underestimated due to the challenge of finding good evidence (Simons 2011); on the other hand, the evolution of bet-hedging might be truly constrained by further, unknown costs. Unfortunately, there is no theoretical framework that discusses potential costs and limits of bet-hedging. There is, however, a larger body of theory on a related topic, namely on costs and limits of phenotypic plasticity (DeWitt et al. 1998, Van Kleunen and Fischer 2005, Auld et al. 2009, Murren et al. 2015), which I will apply to bet-hedging.

According to the conceptual framework, true costs of plasticity need to be separated from phenotype-environment mismatches. A plastic organism that is imperfectly matched to the environment is still better adapted than a canalized organism, which does not fit at all to one environment. Thus, mismatches with the environment represent the limit of an adaptive strategy, and cannot be considered true costs of plasticity. The real costs of phenotypic plasticity can then be split into global (maintenance) and local (production) costs. Maintenance costs are independent of the environment, and arise from the ability to be plastic *per se*, e.g., having the machinery to detect environmental change. Production costs, on the other hand, arise only when phenotypic plasticity is expressed. I argue that this discussion on costs and limits is very similar for bet-hedging.

In accordance with the discussion on phenotypic plasticity, true costs of bet-hedging need to be separated from limits of the otherwise adaptive strategy: By inducing sub-optimal phenotypes, bet-hedging decreases the fitness in an average environment. This decrease in arithmetic mean fitness is not a true cost, but the core of the insurance strategy that increases fitness over longer times, i.e., geometric mean fitness (Simons 2011).

Similar to costs of phenotypic plasticity, costs of bet-hedging can be split into global (maintenance) and local (production) costs. I hypothesize that maintenance costs manifest in a lower overall fitness, because bet-hedging requires a mechanism to generate variability. Bet-hedging could for example be achieved by high sensitivity to small environmental change (microplasticity), as has been observed in the response of seeds to germination conditions (Simons and Johnston 2006). An elevated sensitivity suggests a more elaborate machinery to detect change, and thus higher maintenance costs compared to a non-hedging genotype. Production costs, on the other hand, arise only when the bet-hedging trait is expressed. For example, bet-hedging can be achieved by stochastic processes that disturb developmental pathways during development. Developmental instability has been invoked as source of adaptive variance (Simons and Johnston 1997,

Woods 2014, Dueck et al. 2016), but developmental instability is also one of the costs discussed for phenotypic plasticity (DeWitt et al. 1998). There is no empirical evidence for this kind of cost and it was dismissed for being no true cost of phenotypic plasticity (Auld et al. 2009); however, given the aim of bet-hedging (to induce variance), one should reconsider developmental instability as production costs for bet-hedging. As far as I know, maintenance and production costs of bet-hedging have never been measured.

Aphids as models for bet-hedging

One possible bet-hedging mechanism is stochastic polyphenism, i.e. a stochastic choice of alternative phenotypes (Halkett et al. 2004). One of the most drastic examples for polyphenisms occurs in aphids (Brisson and Stern 2006), because they change reproductive modes in response to the environment. During summer, aphids reproduce by viviparous parthenogenesis. When days become shorter in autumn, most clones in temperate climates switch to production of sexual forms (Dixon and Glen 1971, Lamb and Pointing 1972), because the eggs can overwinter whereas live-born nymphs do not tolerate cold temperatures (Simon et al. 2002). There is considerable variability in the timing of switching, which correlates with environmental variability as predicted by bet-hedging theory (Halkett et al. 2004). While this correlation is a good starting point to study bet-hedging, it is relatively weak evidence (Simons 2011), and other explanations, such as higher clone diversity in more variable climates, cannot be ruled out. Even though variance in reproductive mode switches occurs also in laboratory settings (Lamb and Pointing 1972), it has so far not been assessed systematically. Hence, aphids are good candidates to study bet-hedging in detail.

Project description

With this research idea I want to ask whether seasonal polyphenism is a bet-hedging strategy, and whether its evolution is hampered by fitness costs. I am looking for collaborations, as well as a working environment and research team for a postdoctoral project.

Aphids reproduce asexually over summer, and switch to production of sexual forms when the days shorten. The response to day length follows a logistic curve (Fig. 1), and during a transitional period only a fraction of aphids is induced to produce sexual offspring (Dixon and Glen 1971, Lamb and Pointing 1972), despite being genetically identical and having been reared under the same conditions. I propose that the width of the transitional period is a bet-hedging trait, i.e. that aphids from variable climates spread the transition to sexual offspring more than lines from more constant climates. I thus want to estimate the transitional period (the slope of the logit curve) by subjecting at least 12 aphid clones from different environments to eight different day lengths. I will then assess maintenance and production costs of bet-hedging (Fig. 2). First, I will compare fecundity of bet-hedging and non-hedging clones under long-day conditions, hypothesizing that bet-hedging is associated with lower fecundity even without expression of the trait. Secondly, I will test whether the fitness of bet-hedgers decreases with shortening day lengths (production

costs). Lastly, I will calculate the optimal amount of bet-hedging in all environments, based on environmental unpredictability, growth rates, and fitness costs of bet-hedging. I predict that the degree of bet-hedging of the studied aphid lines optimizes geometric mean fitness in their respective environment.

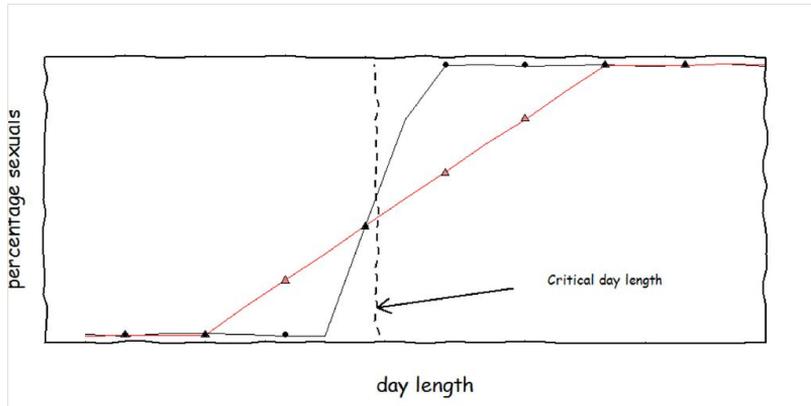


Figure 1.

Phenotypic variance in sexual offspring production. When aphids are subjected to different day lengths, the induction of sexual offspring follows a logistic curve. Near the critical day length (where 50% of the offspring are sexual) there is a transient period in which the choice of offspring type is stochastic. I expect that clones from predictable (black, circles) and unpredictable (red, triangles) environments differ in slope of day length response and thus in the extent of the transient period. In total, 12 clones, each from a different environment, will be tested.

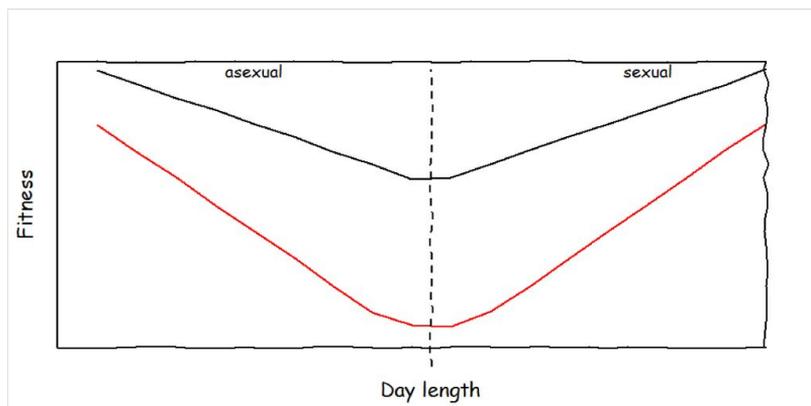


Figure 2.

Maintenance and production costs of bet-hedging. I expect that aphids which invest into bet-hedging produce offspring of lower quality, irrespective of environmental conditions (maintenance costs). In addition, I expect that the costs increase when the bet-hedging trait is expressed (production costs). To test these hypotheses, the data will be analysed separately for sexual and parthenogenetic parents (dashed line = critical day length).

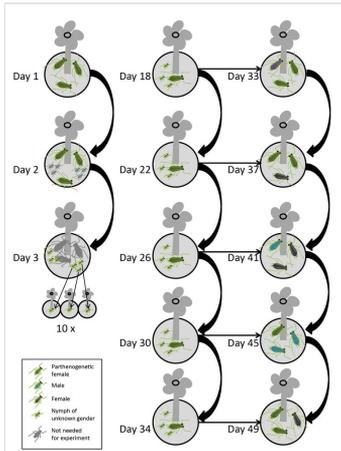


Figure 3.

Intended setup of the main experiment. The focal generation will be kept on individual plants for its full lifetime (middle column), starting two days before birth (left column). All offspring will be raised into adults (right column) to determine the reproductive mode of their parents.

Implementation

Below I propose one potential research plan for the main experiment. Methodology, choice of species and origin of aphid clones are all amendable to change, as they depend on the infrastructure and location of the host institute, on funding and on further collaborations. I first assume that I will collect *Acyrtosiphon pisum* from various locations of Europe, and that the experiment will be split into four smaller experiments with two day length treatments each (for a total of eight day lengths) to accommodate for space limitations. I will then address potential variations of the methodology in the next section.

Methodology

Origin of clones

To obtain aphids with sufficiently different environmental and genetic backgrounds, I require aphid lines originating from a larger regional scale. Nevertheless, to compare the spread of reproductive mode switch in a single experiment, the different lines need to be induced at a similar mean (critical) day length, which correlates with latitude (Smith and MacKay 1990). Hence, I need aphids from a single latitude but various longitudes, for example from Poland, Czech republic, Germany, the Netherlands and Belgium (Fig. 4, [Google Maps](#)). I will collect several aphid lines in 14 sampling areas, and use one line per sampling area in later experiments. With one day per sampling area, the aphids can be collected within two weeks, so expenses for traveling (3300 km) and accommodation amount to approximately

3000€. I have experience in aphid identification, and the species *Acyrtosiphon pisum* and *Megoura viciae* can be readily identified in the field. All clones will be tested under short day conditions to confirm that the obtained lines are holocyclic, and to select aphids with homogenous mean day length.

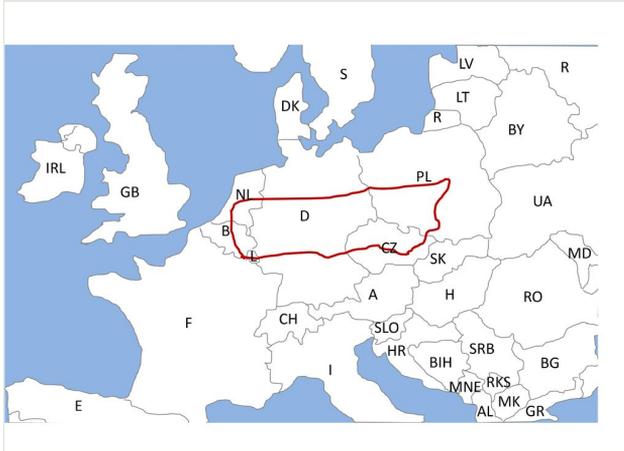


Figure 4.

Map of Europe, with intended sampling location.

Climate data

The experiment requires aphid lines from a gradient of winter unpredictability. This has been defined by Halkett et al. (2004) as between-year standard deviation in onset of winter. According to this definition winter arrives at the moment when a regression on monthly mean temperatures crosses 12 °C. The European monthly mean temperatures from 2000-2010 (5x5 km) are freely available from the [DWD \(German Weather Service\)](#).

While the standard deviation in onset of winter can be easily calculated, it neglects adaptive phenotypic plasticity. For example, the response to day length is modulated by temperature (Dixon and Glen 1971, Lamb and Pointing 1972), so it is delayed in warmer years with late winter onset. I will explore the use of temporal autocorrelation in autumn temperatures as alternative way to define winter unpredictability.

Experiment

The procedure for 12 clones kept at two day lengths is as follows (Fig. 3): I will place 10 individuals ('grandparents') per clone on two plants, and move the plants to two climate chambers with different day lengths. The offspring born on the third day are the focal individuals ('parents') and will be kept. 10 parents per clone and chamber will be randomly selected, placed individually on a new plant (120 plants per chamber) and allowed to mature. When adult, the parents will be moved to new plants every 4 days, and the old plants with offspring will be kept. The sexuality of the next generation ('offspring'; parthenogenetic, male or female) will indicate the reproductive mode of their parents. This

requires 240 new plants every 4 days, and about 1200 plants in total. When the offspring are adult (from approximately day 33 to day 49), they will be examined at low magnification, and their number will be used as fitness estimate. With an average of five minutes per sample, it takes 100 hours to identify all 1200 samples, but the offspring will be frozen and can be examined later. As time allows, samples will be thawed and size measurements will be made.

Hypothesis 1: variance in reproductive modes correlates with winter unpredictability

When plotting the percentage of sexual offspring against day length, I will obtain a logistic curve as in Fig. 1. The slope of the curves (i.e. width of transitional photoperiods) will vary among clones from different backgrounds, and I expect the slope to correlate with the environmental unpredictability of their origin. I will thus apply a generalized linear mixed-effects model with binomial distribution. The percentage of sexuals is predicted by day length treatment, the environment in which the aphids were sampled, and their interaction:

glmer (Induction ~ treatment * environment + (1 | mother/environment), family = binomial)

A significant interaction will support the hypothesis that the transient period correlates with environmental unpredictability. In addition, a significant positive effect of environment alone would indicate that clones from the most unpredictable environments also take riskier (later) strategies, as the modelling approach of Halkett et al. (2004) suggests.

Bet-hedging could be achieved by two different modes: First, a single mother aphid can produce both sexual and asexual offspring. Secondly, each mother can produce only one type of offspring, but the choice of the type differs among genetically identical mothers. Literature suggests that mixed families exist in *A.pisum* (Lamb and Pointing 1972), so I calculate the percentage of sexual offspring, corrected for mother identity. If all adults produce either only sexual or only asexual forms, and no mixed families exist, the model can be reduced by the random term – the response variable is then the fraction of mothers producing sexual offspring.

Hypothesis 2: Bet-hedgers suffer maintenance and production costs

Because photoperiodic induction requires rearing all offspring I will obtain detailed data on life-history traits. I hypothesize that clones which cope with high environmental unpredictability suffer from generally reduced fertility (maintenance costs), or from higher production costs when reared near the critical day length that induces transition from asexual to sexual reproduction (Fig. 2).

Because development times and fecundity per day of the parent aphids are known, I construct life history tables and derive population growth based on a Leslie matrix, which gives a detailed account of aphid fitness (Joschinski et al. 2015). I will compare the fitness of aphids that were reared under full long days with aphids that were reared under the critical day length, but still produced asexual offspring. In addition, I will compare the aphids that were marginally induced to produce sexual offspring with those reared under short

days. Both sexual and asexual datasets will be supplemented by size measurements of the offspring for a better measure of their respective reproductive value.

For both dataset I will apply the model:

Fitness \sim day_length * environment + (1 | mother/environment)

A significant interaction of day length and environment is evidence for production costs (increased costs close to critical day length). If there is a significant effect of environment, this will be evidence for maintenance costs (generally reduced fitness).

Hypothesis 3: The degree of bet-hedging matches quantitatively with environmental variance

Strong evidence for bet-hedging is provided by the observation that phenotypic variance can be quantitatively predicted by environmental variation (Simons 2011). I will extend a model by Halkett et al. (2004) by maintenance and production costs, and calculate the optimal phenotypic variance for each environment. I will then test whether the observed phenotypic variability provides a quantitative fit with the optimum.

Adaptations

Depending on host institute and collaborative projects, several details of the experiment can be adapted. Below I describe potential variations from the research plan.

Species

Because polyphenism in reproductive modes is a primitive feature of the Aphidoidea (Moran 1992), the proposed experiments can principally be carried out with any aphid species with a holocyclic life cycle. Three species seem particularly suitable for the experiments: The pea aphid, *Acyrtosiphon pisum*, the bird cherry-oat aphid, *Rhopalosiphum padi*, and the vetch aphid, *Megoura viciae*.

A.pisum is an emerging model organism in ecology (Huang and Qiao 2014) and developmental biology (Brisson and Stern 2006). It is relatively large, the genome has been sequenced and annotated (The International Aphid Genomics Consortium 2010), and the polyphenism has been studied in detail (e.g., Le Trionnaire et al. 2008, Le Trionnaire et al. 2013). The bird cherry – oat aphid, *Rhopalosiphum padi*, is not only an important cereal pest, but was also used to parametrize the so far only model on bet-hedging in aphids (Halkett et al. 2004). The life cycle of this host-alternating species is however more complicated. Short days do not induce aphids to directly produce sexual forms, but to produce winged gynoparae, which will migrate to the winter host before producing sexuals. Lastly the most detailed analysis of the reproductive mode switch has been conducted on *M. viciae* (Lees 1959, Lees 1960, Lees 1963). All three species are common in agricultural landscapes throughout Europe (Blackman and Eastop 2000), and the choice among the three model organisms will depend on the work environment.

Origin of clones

The experiment requires aphid lines from several locations throughout Europe. I plan to sample aphid lines shortly before the experiments, because aphids can evolve quickly despite being asexual (Thieme and Dixon 2015), and artificial selection under constant environments might have selected against bet-hedging. Nevertheless, I would be happy for suggestions on obtaining aphid lines that have been collected recently.

Logistics

The experiment is logistically challenging. It requires frequently transferring aphids from 240 plants to new plants, and I need 1200 host plants in total. The procedure would be considerably easier, if the parent's reproductive mode was known without having to rear all offspring. If the sexuality of the offspring could be determined on newly born nymphs, it would reduce the number of plants to 240 and reduce the time from 49 to 34 days. Thus, I would be happy for any suggestions to determine reproductive modes of young offspring morphologically.

In *A. pisum*, the reproductive mode of the parents could also be determined by analysing gene expression of the young offspring (Le Trionnaire et al. 2012). This method is likely more expensive than rearing all offspring, but would allow studying individuals reared at the critical day length. This treatment allows insights into molecular regulation of the polyphenism (photoperiodism), and I welcome collaborations on this topic.

Location

I am looking for collaborators with knowledge in aphid biology and/or bet-hedging theory, and for a research environment that has at least two climate chambers and sufficient greenhouse space to rear about 1200 plants. The project will require approximately 3000€ to collect aphids, as well as small funds for aphid and plant rearing, and for student helpers for general maintenance of aphid clones and plants.

Further considerations

The proposed research project carries the danger that aphids do not hedge their bets, which makes an analysis of costs of bet-hedging obsolete. The phenotypic variance I want to assess has however also been observed in a single aphid clone before (Lamb and Pointing 1972). I have used the bet-hedging model by Halkett et al. 2004 to predict the optimal phenotypic variance for this clone from Markham, Ontario. According to the last 50 years of a weather dataset of the nearby town Toronto (Vincent et al. 2012), the winter unpredictability was 4.4, so the bet-hedging model suggests 11 days of mixed reproduction. The photoperiod in which mixed reproduction occurs (i.e. variance in sexual induction) was not assessed systematically by Lamb and Pointing (1972), but Fig.2 suggests a range of about 30 minutes day length change, which corresponds to 11 days. Thus, the laboratory results from the single clone seem to agree with those predicted by the bet-hedging model.

Preliminary work

Preliminary work during my doctoral thesis (to be submitted in 2016) focused on the constraints of the sexual polyphenism. Aphids are generally considered to benefit from climate change by extending their phenology into early spring and late autumn. During the doctoral thesis I asked whether aphids can use the novel temperature-day length combinations efficiently. I demonstrated that aphids suffer fitness constraints under short days, so the evolution of phenology might be constrained (Joschinski et al. 2015a). Further research revealed that aphids are day-active (Joschinski et al. 2016), which explains the fitness constraints of short days by a limited time budget. Apart from this focus on behavioral ecology and physiology, I also received training in evolutionary biology (Joschinski et al. 2015b).

Project-related publications

Joschinski J, Hovestadt T, Krauss J (2015a) Coping with shorter days: do phenology shifts constrain aphid fitness? *PeerJ* 3: e1103. DOI: [10.7717/peerj.1103](https://doi.org/10.7717/peerj.1103).

Joschinski J, Beer K, Helfrich-Förster C, Krauss J (2016) Pea aphids (Hemiptera: Aphididae) have diurnal rhythms when raised independently of a host plant. *Journal of Insect Science* 16 (31):1-5. DOI: [10.1093/jisesa/iew013](https://doi.org/10.1093/jisesa/iew013).

Other publications

Joschinski J, van Kleunen, M, & Stift, M. (2015b) Costs associated with the evolution of selfing in North American populations of *Arabidopsis lyrata*? *Evolutionary Ecology* 29 (5): 749-764. DOI: [10.1007/s10682-015-9786-3](https://doi.org/10.1007/s10682-015-9786-3)

Expected results and impact

I expect that the experiment outlined in this proposal will be the first to demonstrate a long-term fitness advantage of bet-hedging in insects. Furthermore, with the experiment I quantify the production costs and the maintenance costs of bet-hedging. I expect that the results of the experiment will be summarized in one publication (e.g. in *American Naturalist* or *Evolution*).

Depending on further collaborations, the main experiment could be supplemented by further studies. For example, I could assess the gene expression of aphids reared under the critical day length. The data could be used to study the switch in reproductive modes (photoperiodism), which would result in a further publication.

Acknowledgements

This research idea greatly benefitted from stimulating discussions within the DFG-funded collaborative research center “SFB 1047 insect timing”. I particularly thank Thomas Hovestadt, Oliver Mitesser, Christophe Gadenne and Jochen Krauss for helpful comments on the manuscript.

Funding program

Funding was provided by the German Research Foundation (DFG), collaborative research center SFB 1047 “Insect timing”,

Grant title

Project C3.

Conflicts of interest

The author declares no conflict of interest.

References

- Auld JR, Agrawal AA, Relyea RA (2009) Re-evaluating the costs and limits of adaptive phenotypic plasticity. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 277 (1681): 503-511. DOI: [10.1098/rspb.2009.1355](https://doi.org/10.1098/rspb.2009.1355)
- Blackman RL, Eastop VF (2000) *Aphids on the world's crops*. John Wiley & Sons, Chichester, England, 476 pp.
- Brisson J, Stern D (2006) The pea aphid, *Acyrtosiphon pisum*: an emerging genomic model system for ecological, developmental and evolutionary studies. *Bioessays* 28 (7): 747-755. [In en]. DOI: [10.1002/bies.20436](https://doi.org/10.1002/bies.20436)
- Charmantier A, McCleery R, Cole L, Perrins C, Kruuk LB, Sheldon B (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320 (5877): 800-803. [In en]. DOI: [10.1126/science.1157174](https://doi.org/10.1126/science.1157174)
- Chevin L, Lande R, Mace G (2010) Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. *PLoS Biology* 8 (4): 20120089. DOI: [10.1371/journal.pbio.1000357](https://doi.org/10.1371/journal.pbio.1000357)
- Cohen D (1966) Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12 (1): 119-129. DOI: [10.1016/002f2-5193\(66\)90188-3](https://doi.org/10.1016/002f2-5193(66)90188-3)
- DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution* 13 (2): 77-81. [In eng]. DOI: [10.1016/S0169-5347\(97\)01274-3](https://doi.org/10.1016/S0169-5347(97)01274-3)

- Dixon AFG, Glen DM (1971) Morph determination in the bird cherry-oat aphid, *Rhopalosiphum padi* L. *Annals of Applied Biology* 68 (1): 11-21. [In eng]. DOI: [10.1111/j.1744-7348.1971.tb04633.x](https://doi.org/10.1111/j.1744-7348.1971.tb04633.x)
- Dueck H, Eberwine J, Kim J (2016) Variation is function: Are single cell differences functionally important? *Bioessays* 38 (2): 172-180. DOI: [10.1002/bies.201500124](https://doi.org/10.1002/bies.201500124)
- Halkett F, Harrington R, Hulle M, Kindlmann P, Menu F, Rispe C, Plantegenest M (2004) Dynamics of production of sexual forms in aphids: theoretical and experimental evidence for adaptive "coin-flipping" plasticity. *The American Naturalist* 163 (6): 112-25. [In eng]. DOI: [10.1086/383618](https://doi.org/10.1086/383618)
- Huang X, Qiao G (2014) Aphids as models for ecological and evolutionary studies. *Insect Science* 21 (3): 247-250. DOI: [10.1111/1744-7917.12130](https://doi.org/10.1111/1744-7917.12130)
- IPCC (2014) *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland, 151 pp.
- Jackson S, Betancourt J, Booth R, Gray S (2009) Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences* 106: 19685-19692. DOI: [10.1073/pnas.0901644106](https://doi.org/10.1073/pnas.0901644106)
- Joschinski J, Hovestadt T, Krauss J (2015a) Coping with shorter days: do phenology shifts constrain aphid fitness? *PeerJ* 3: e1103. [In eng]. DOI: [10.7717/peerj.1103](https://doi.org/10.7717/peerj.1103)
- Joschinski J, Kleunen Mv, Stift M (2015b) Costs associated with the evolution of selfing in North American populations of *Arabidopsis lyrata*? *Evolutionary Ecology* 29 (5): 749-764. DOI: [10.1007/s10682-015-9786-3](https://doi.org/10.1007/s10682-015-9786-3)
- Joschinski J, Beer K, Helfrich-Förster C, Krauss J (2016) Pea aphids (Hemiptera: Aphididae) have diurnal rhythms when raised independently of a host plant. *Journal of Insect Science* 16 (1): 1-5. DOI: [10.1093/jisesa/iew013](https://doi.org/10.1093/jisesa/iew013)
- Karell P, Ahola K, Karstinen T, Valkama J, Brommer J (2011) Climate change drives microevolution in a wild bird. *Nature Communications* 2: 208. DOI: [10.1038/ncomms1213](https://doi.org/10.1038/ncomms1213)
- Lamb RJ, Pointing PJ (1972) Sexual morph determination in the aphid, *Acyrtosiphon pisum*. *Journal of Insect Physiology* 18 (10): 2029-2042. DOI: [10.1016/0022-1910\(72\)90170-9](https://doi.org/10.1016/0022-1910(72)90170-9)
- Lees AD (1959) The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Buckton—I. *Journal of Insect Physiology* 3 (2): 92-117. DOI: [10.1016/0022-1910\(59\)90024-1](https://doi.org/10.1016/0022-1910(59)90024-1)
- Lees AD (1960) The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Buckton—II. The operation of the 'interval timer' in young clones. *Journal of Insect Physiology* 4 (2): 154-175. DOI: [10.1016/0022-1910\(60\)90078-0](https://doi.org/10.1016/0022-1910(60)90078-0)
- Lees AD (1963) The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Buckton—III. Further properties of the maternal switching mechanism in apterous aphids. *Journal of Insect Physiology* 9 (2): 153-164. DOI: [10.1016/0022-1910\(63\)90067-2](https://doi.org/10.1016/0022-1910(63)90067-2)
- Le Trionnaire G, Wucher V, Tagu D (2013) Genome expression control during the photoperiodic response of aphids. *Physiological Entomology* 38 (2): 117-125. [In English]. DOI: [10.1111/phen.12021](https://doi.org/10.1111/phen.12021)

- Le Trionnaire G, Hardie J, Jaubert-Possamai S, Simon J, Tagu D (2008) Shifting from clonal to sexual reproduction in aphids: physiological and developmental aspects. *Biology of the Cell* 100 (8): 441-451. [In en]. DOI: [10.1042/bc20070135](https://doi.org/10.1042/bc20070135)
- Le Trionnaire G, Jaubert-Possamai S, Bonhomme J, Gauthier JP, Guerneq G, Le Cam A, Legeai F, Monfort J, Tagu D (2012) Transcriptomic profiling of the reproductive mode switch in the pea aphid in response to natural autumnal photoperiod. *Journal of Insect Physiology* 58 (12): 1517-24. [In eng]. DOI: [10.1016/j.jinsphys.2012.07.009](https://doi.org/10.1016/j.jinsphys.2012.07.009)
- Moran NA (1992) The evolution of aphid life cycles. *Annual Review of Entomology* 37 (1): 321-348. DOI: [10.1146/annurev.en.37.010192.001541](https://doi.org/10.1146/annurev.en.37.010192.001541)
- Murren CJ, Auld JR, Callahan H, Ghalambor CK, Handelsman CA, Heskell MA, Kingsolver JG, Maclean HJ, Masel J, Maughan H, Pfennig DW, Relyea RA, Seiter S, Snell-Rood E, Steiner UK, Schlichting CD (2015) Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity* 115 (4): 293-301. DOI: [10.1038/hdy.2015.8](https://doi.org/10.1038/hdy.2015.8)
- Simon J, Rispe C, Sunnucks P (2002) Ecology and evolution of sex in aphids. *Trends in Ecology & Evolution* 17 (1): 34-39. DOI: [10.1016/s0169-5347\(01\)02331-x](https://doi.org/10.1016/s0169-5347(01)02331-x)
- Simons A (2011) Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings of the Royal Society B: Biological Sciences* 278 (1712): 1601-1609. DOI: [10.1098/rspb.2011.0176](https://doi.org/10.1098/rspb.2011.0176)
- Simons AM, Johnston MO (1997) Developmental instability as a bet-hedging strategy. *Oikos* 80 (2): 401-406. [In English]. DOI: [10.2307/3546608](https://doi.org/10.2307/3546608)
- Simons AM, Johnston MO (2006) Environmental and genetic sources of diversification in the timing of seed germination: implications for the evolution of bet hedging. *Evolution* 60 (11): 2280-2292. DOI: [10.1554/05-396.1](https://doi.org/10.1554/05-396.1)
- Smith MAH, MacKay PA (1990) Latitudinal variation in the photoperiodic responses of populations of pea aphid (Homoptera: Aphididae). *Environmental Entomology* 19 (3): 618-624. DOI: [10.1093/ee/19.3.618](https://doi.org/10.1093/ee/19.3.618)
- The International Aphid Genomics Consortium (2010) Genome sequence of the Pea aphid *Acyrtosiphon pisum*. *PLoS Biology* 8 (2): e1000313. DOI: [10.1371/journal.pbio.1000313](https://doi.org/10.1371/journal.pbio.1000313)
- Thieme T, Dixon AFG (2015) Is the response of aphids to alarm pheromone stable? *Journal of Applied Entomology* 139 (10): 741-746. DOI: [10.1111/jen.12262](https://doi.org/10.1111/jen.12262)
- Tufto J (2015) Genetic evolution, plasticity, and bet-hedging as adaptive responses to temporally autocorrelated fluctuating selection: A quantitative genetic model. *Evolution* 69 (8): 2034-2049. DOI: [10.1111/evo.12716](https://doi.org/10.1111/evo.12716)
- Urban M (2015) Accelerating extinction risk from climate change. *Science* 348 (6234): 571-573. DOI: [10.1126/science.aaa4984](https://doi.org/10.1126/science.aaa4984)
- Van Kleunen M, Fischer M (2005) Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* 166 (1): 49-60. DOI: [10.1111/j.1469-8137.2004.01296.x](https://doi.org/10.1111/j.1469-8137.2004.01296.x)
- Vedder O, Bouwhuis S, Sheldon B (2013) Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS Biology* 11 (7): 1001605. DOI: [10.1371/journal.pbio.1001605](https://doi.org/10.1371/journal.pbio.1001605)
- Vincent L, Wang X, Milewska E, Wan H, Yang F, Swail V (2012) A second generation of homogenized Canadian monthly surface air temperature for climate trend analysis. *Journal of Geophysical Research: Atmospheres* 117 (18): D18110. DOI: [10.1029/2012JD017859](https://doi.org/10.1029/2012JD017859)

- Woods HA (2014) Mosaic physiology from developmental noise: within-organism physiological diversity as an alternative to phenotypic plasticity and phenotypic flexibility. *Journal of Experimental Biology* 217 (1): 35-45. [In English]. DOI: [10.1242/jeb.089698](https://doi.org/10.1242/jeb.089698)