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SHORT COMMUNICATION

Large-scale migration synchrony between parasitoids and their host

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Abstract. 1. Parasitoids are a valuable group for conservation biological control. In their role as regulators of aphid pests, it is critical that their lifecycle is synchronised with their hosts in both space and time. This is because a synchronised parasitoid community is more likely to strengthen the overall conservation biological control effect, thus damping aphid numbers and preventing potential outbreaks. One component of this host–parasitoid system was examined, that of migration, and the hypothesis that peak summer parasitoid and host migrations are synchronised in time was tested.

2. *Sitobion avenae* Fabricius and six associated parasitoids were sampled from 1976 to 2013 using 12.2-m suction-traps from two sites in Southern England. The relationship between peak weekly *S. avenae* counts and their parasitoids was quantified.

3. Simple regression models showed that the response of the peak parasitoids to the host was positive: generally, more parasitoids migrated with increasing numbers of aphids. Further, when averaged over time, the parasitoid migration peak date corresponded with the aphid migration peak. The co-occurrence of the peaks was between 51% and 64%. However, the summer peak in aphid migration is not steadily shifting forward with time unlike spring first flights of aphids. Cross-correlation analysis showed that there were no between-year lagged effects of aphids on parasitoids.

4. These results demonstrate that the peak in migration phenology between host and parasitoid is broadly synchronised within a season. Because the threshold temperature for flight ($> 12\,^{\circ}\mathrm{C}$) was almost always exceeded in summer, the synchronising agent is likely to be crop senescence, not temperature. Studies are needed to assess the effects of climate change on the mismatch potential between parasitoids and their hosts.

Key words. Aphidiinae, long-term monitoring, phenology, population dynamics, *Sitobion avenae*, suction-trap.

Introduction

The ‘Red Queen Hypothesis’ infers that parasitoid–host relationships are under a strong selection pressure to adapt and was proposed by Van Valen (1973) to emphasise the importance of biotic interactions in driving evolution. In the context of host–parasitoid relationships, The Red Queen Hypothesis predicts a co-evolutionary arms race: hosts must constantly adapt their behavioural and chemical defences to avoid becoming parasitised. Similarly, parasitoids must also evolve to overcome the newly acquired host defences that are being employed if they are to continue into the next generation. The overall effect is that the probability of extinction remains fairly constant over time because both host and parasitoid are hypothesised to be co-evolving at the same rate (Brockhurst *et al.*, 2014). As such, The Red Queen Hypothesis maintains high levels of genetic diversity because ‘fast-evolving’ genes associate with the arms race (Brockhurst *et al.*, 2014). Arguably though, parasitoids are less resilient to climate or landscape change than their hosts (Hance *et al.*, 2007; Harrington *et al.*, 2007; Jeffs & Lewis, 2013). The consequences of asynchrony are clear: if there were to be a perfect mismatch (i.e. an absence of parasitism), aphid populations could be seven times larger within a season because they would be at no risk of parasitism (Dixon, 1987).

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In this study, we analyse the relationship between the migrations of the English grain aphid *Sitobion avenae* Fabricius (Hemiptera: Aphididae) and its associated Aphidiinae parasitoids using data from suction-trap sites located in southern England at Writtle and Rothamsted. The grain aphid is a worldwide pest that infests cereals and reduces crop yield and quality through direct feeding and virus transmission (Vickerman & Wratten, 1979; Dixon, 1987; Brewer & Elliott, 2004). The aphid's host plants include wheat and other cereals that are cultivated across the world's temperate zone. In 2014, cereals were projected to yield 2480 million tonnes globally, providing food for billions of people (FAO, 2014). However, yields are greatly reduced by aphid feeding. For example, owing to aphid damage average yields have been estimated to fall by 700 000 tonnes annually across Europe and it has also been shown that aphids can cost the American economy up to $274 million (Dedryver *et al.*, 2010). Recently, chemical intervention by farmers has triggered aphid resistance mechanisms to pyrethroids that are commonly used to protect crops against aphid feeding damage (Foster *et al.*, 2014). The constant evolution and resistance to chemical control and the EU-enforced reduction of insecticides available to farmers both serve to highlight the value of conservation biological control as a tool to help regulate aphid populations (Schmidt *et al.*, 2003; Meiners & Peri, 2013).

Schmidt *et al.* (2003) showed that parasitoid wasps provided the most important contribution towards suppression of aphid densities and rated their importance above generalist predators, perhaps because parasitoids have evolved specialised biochemical mechanisms for detecting their hosts (Meiners & Peri, 2013). Studies have shown that the proportion of parasitised *S. avenae* within the wheat crop varies depending on the year and location but ranges from 21% to 50% demonstrating their regulatory effect as a group [e.g. Walton *et al.*, 1990 (50%); Höller *et al.*, 1993 (33%); Macfadyen *et al.*, 2009 (44%); Traugott *et al.*, 2012 (21.4%)]. The parasitoids that are associated with the grain aphid in the U.K. include the following species: *Aphidius ervi* Haliday, *A. rhophalosiphi* de Stefani-Perez, *A. avenae* Haliday, *A. uzbekistanicus* Luzhetzki, *A. frumentarius* Latteur, *Ephedrus plagiator* (Nees), *Praon gallicum* Stary, *P. volucre* (Haliday), *Aphelinus abdominalis* (Dalman), *Toxacres deltiger* (Haliday), *Diaretiella rapae* (McIntosh), and *Lysiphlebus fabarum* (Marshall) (Powell, 1982; Traugott *et al.*, 2008).

The most important parasitoids of *S. avenae* belong to the Aphidiinae subfamily (Hymenoptera: Braconidae) that are solitary koinobionts, ovipositing one egg per host, rarely two or more (Chua *et al.*, 1990), killing them before the host can reach maturity (Stary, 1970). This parasitoid–host interaction depends on population synchrony that itself is subject to exogenous forces, such as climate, weather, and the agricultural landscape that drive populations at different rates depending on how plastic and adaptable species have become (Harrington *et al.*, 2007; Schellhorn *et al.*, 2014). Generally, studies have shown a wide-scale climate impact on plants and animals (Root *et al.*, 2003; Thackeray *et al.*, 2010; Rafferty *et al.*, 2013), but the effects of a warming climate on host–parasitoid interactions are still not well known (Jeffs & Lewis, 2013). During the last five decades, it has been shown that aphid migrations (first flights, fifth percentile flights) are getting earlier, often much faster than those of plants and mammals (Harrington *et al.*, 2007; Thackeray *et al.*, 2010; Bell *et al.*, 2015). It is not yet understood if parasitoids are tracking this phenological response by shifting their migrations earlier to match aphid flights or migrating later thus creating a 'mismatch' over time.

This paper is not a formal test of the Red Queen Hypothesis or the Trophic Asynchrony (mismatch) Hypothesis because our analyses are correlative in nature. However, using an extensive time series over multiple decades, we test (i) whether parasitoid migrations are related to aphid migrations, (ii) whether these are migrations are influenced by temperature, if at all, (iii) if a shift in host and parasitoid numbers forward is evident, indicating an adaption to a changing climate, and, (iv) if migration synchrony is present, supporting the view that no trophic disjuncture has emerged.

Materials and Methods

The Rothamsted Insect Survey (RIS) operates a network of suction traps that continuously measure the aerial density of flying aphids and other insects, sampling at the logarithmic mean height of aphid flight (12.2 m) and providing daily records during the aphid season (April to November), and weekly records at other times (Macaulay *et al.*, 1988). Historical data on aphid numbers are readily available from the foundation of the RIS in 1964. Small parasitoids are also effectively sampled by the suction traps, in that they are well represented in terms of species found at a ground level. However, it has yet to be shown how well parasitoid migration at 12.2 m reflects numbers on the ground. What is known is that parasitoids, including *Aphidius* sp., migrate in good numbers at much higher altitudes of at least 200 m in southern England (Chapman *et al.*, 2004; J. Chapman, unpublished). We conclude, therefore, that suction traps fall well within the altitudinal range of possible parasitoid flight.

Our study used digital (i.e. database records of previously identified aphids from the samples) and archived suction-trap samples (i.e. the non-aphid fraction that includes parasitoids that have yet to identified) from Rothamsted (Hertfordshire: 51.806°, −0.360°) and Writtle (Essex: 51.733°, −0.429°). These sites are 55 km apart and located in the south east of England, where wheat and oilseed rape fields dominate the agricultural landscape amongst a patchwork of field margins and permanent grassland, both of which are suitable for aphid overwintering.

To study the relationship between migrating *S. avenae* and its Aphidiinae parasitoids, we selected the peak week when *S. avenae* was most abundant for each site-year between 1975 and 2013 in Writtle and 1982 and 2013 in Rothamsted (Table S1). The month in which the aphid peak week fell was always between the 3-month period starting June and ending in August. We investigated archived samples from the median day of this week, and the median week day 2 weeks either side. As a result, a total of 195 sampling days in Writtle and 165 in Rothamsted were studied for which we also derived the average daily temperature for both sites. The lengths of these time series were constrained by the availability of archived samples that would allow the quantification of parasitoids.

We counted the numbers of Braconidae in the archived samples and then identified the following *S. avenae* parasitoids:

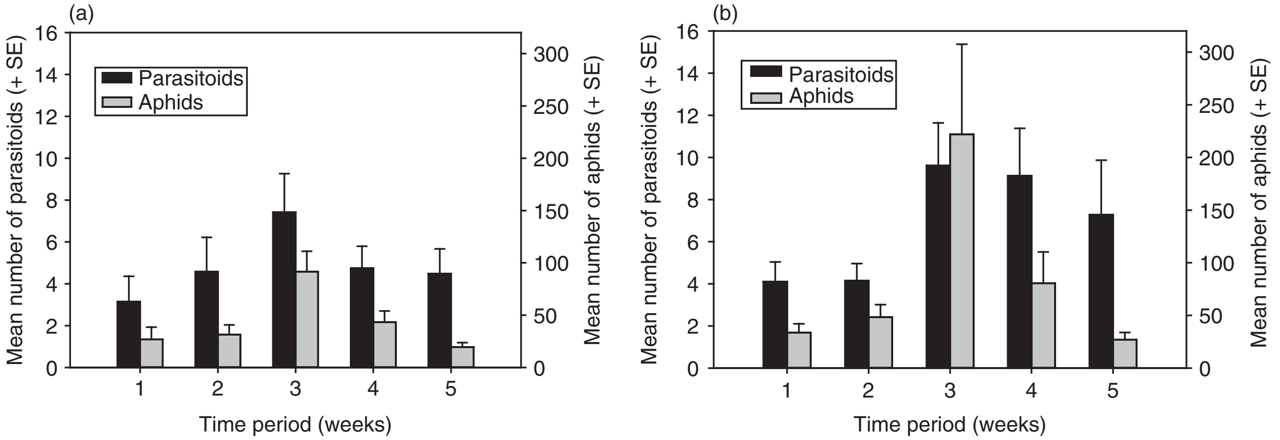

Fig. 1. The mean number of *Sitobion avenae* and its associated parasitoids per sampling period. (a) Rothamsted between 1982 and 2013 and (b) Writtle between 1975 and 2013.

the *A. ervi, A. avenae, E. plagiator, P. volucre, T. deltiger*, and *A. uzbekistanicus* group. *Aphidius uzbekistanicus* is part of a complex species group that cannot reliably be separated morphologically (G. Broad, pers. comm.) and comprises both *A. uzbekistanicus* and *A. rhophalosiphi*.

Average daily temperatures were used to provide a potential mechanistic understanding of what may promote parasitoids and their hosts to migrate. These temperatures were averaged over 1 day for each date and paired with the respective sample to which they related (Table S1). Both Rothamsted and Writtle meteorological stations were used to derive these daily average temperatures.

A simple linear regression (ordinary least squares, OLS) analysis was used to predict paired log parasitoid from log aphid abundance across the full dataset. A significant positive relationship would indicate a degree of synchrony between both populations. Again using OLS, the effect of average daily temperature was tested as a mechanism that was hypothesised to drive the phenologies of both aphid and parasitoids. For each group at each site, independent models that included log aphids or log parasitoids as the response and average daily temperatures as the predictor, were computed. Lastly, to test whether the peak week of aphid abundance had shifted in time, the Julian day of the median week day (Table S1) was regressed against year using OLS. Additionally, cross correlations on the annual abundances of the parasitoid and aphid host were used to detect any lagged year effects (between 1 and 5 years). SigmaPlot 12.0 (Systat Software Inc, Hounslow, U.K.) and GenStat 16 (VSN International Ltd, Hemel Hempstead, U.K.) programs were used.

Results and Discussion

During the sampling period, 22.14% of the 9737 braconid parasitoids recorded were associated with *S. avenae* (approx. 2156) (Powell, 1982; Traugott *et al.*, 2008). There was general statistical agreement that at a distance of 55 km apart, the migrating parasitoid community was broadly similar between Rothamsted and Writtle (Figure S1a,b). Any small differences in proportion could be as a result of the differences in timing of oviposition or local landscape characteristics (Langer *et al.*, 2004). Importantly, the host–parasitoid relationship followed the same pattern: when averaged over the time series, the mean number of parasitoids reached its highest numbers in the period when the mean number of *S. avenae* was also maximised (Fig. 1, time period number 3), suggesting a strong element of temporal synchrony (Fig. 1a,b). Supporting these data were linear regressions that showed a positive relationship between numbers of parasitoids and *S. avenae*. The regressions quantified the rate at which parasitoids responded: per unit change in the log aphid abundance yielded a log change of between 0.220 ± 0.058 and 0.223 ± 0.069 in the parasitoids at Rothamsted ($P = 0.0002$, $r^2 = 0.168$) and Writtle ($P = 0.0008$, $r^2 = 0.157$) respectively. However, there were times when aphids were present but parasitoids did not respond and *vice versa* (Fig. 2 a,b) which might be expected in noisy systems (Ekbom *et al.*, 1992; Klapwijk *et al.*, 2010). We explored whether daily temperatures were a potential mechanism that would explain observed relationships between parasitoids, aphids, and temperature over the whole datasets for both Rothamsted and Writtle. The parasitoid-temperature models suggested that any relationship was effectively random with no apparent slope (Rothamsted: $\beta = 0.0022 \pm$ SE 0.0144, $t = 0.15$, $P = 0.880$. Writtle $\beta = 0.0012 \pm$ SE 0.0145, $t = 0.08$; $P = 0.934$) but as in other studies of aphid migration that link temperature to phenology (Harrington *et al.*, 2007; Bell *et al.*, 2015), aphids were shown to be related to temperature changes (Rothamsted: $\beta = 0.0823 \pm$ SE 0.0221, $t = 3.72$, $P = < 0.001$. Writtle: $\beta = 0.0464 \pm$ SE 0.0210, $t = 2.21$; $P = 0.028$). However, we caution against these models because while they are statistically significant, they only capture 7.3% and 2.0% of the variance respectively, indicating a very high degree of scatter.

These regression results were explicable because the minimum daily temperature threshold that promotes migration is normally always exceeded during summer (June–August) when both parasitoid and host are migrating. At Rothamsted and Writtle, the average daily minimum temperatures were 13.61 °C ± SE 0.29 °C and 14.33 °C ± SE 0.26 °C, respectively.

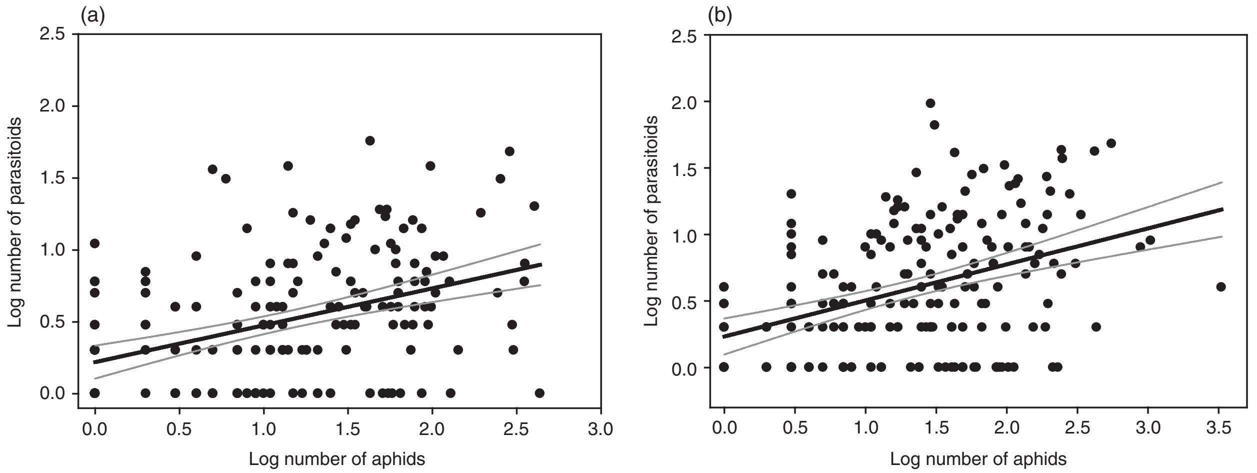

Fig. 2. Linear regressions with 95% confidence intervals between log parasitoids and log *Sitobion avenae* abundances at showing that the host–parasitoid migration peaks are linearly related (a) Rothamsted: per unit change in the log aphid abundances yields a log change of 0.220 ± SE 0.058 in the parasitoids ($r^2 = 0.168$) (b) Writtle: per unit change in the log aphid abundances yields a log change of 0.223 ± SE 0.069 in the parasitoids ($r^2 = 0.157$).

Further, the frequency of temperatures below 12 °C was low and only occurred between 1.5% and 2.4% of the time, depending on location. Although temperature could affect the timing of parasitoid emergence, especially in early spring (van Nouhuys & Lei, 2004; Hance *et al.*, 2007; Klapwijk *et al.*, 2010), temperature does not directly explain the migration synchrony between parasitoids and their host. It is more likely that both host and parasitoids are responding to the effects of crop senescence that causes aphids to leave the crop owing to a reduced feeding potential and parasitoids to migrate because they are responding to a change in crop quality through a change in the density of the host (Schellhorn *et al.*, 2014). At this time, some of the aphids could be carrying a parasite with them: a recent study by Huang *et al.* (2008) demonstrated that migratory alates (winged) of *Myzus persicae* (Sulzer) and *Brevicoryne brassicae* (Linnaeus) captured in the air were shown to be hosting parasitoids. Further, Walton *et al.* (2011) showed, using polyacrylamide gel electrophoresis, that rates of parasitism in airborne alatae *S. avenae* can be detected in Rothamsted Insect Survey suction traps. The rates of parasitism varied between weeks sampled but could be as high as 12%. In other systems, numbers of parasitoids migrating within hosts have been shown to be much lower and around 1% (Derocles *et al.*, 2014).

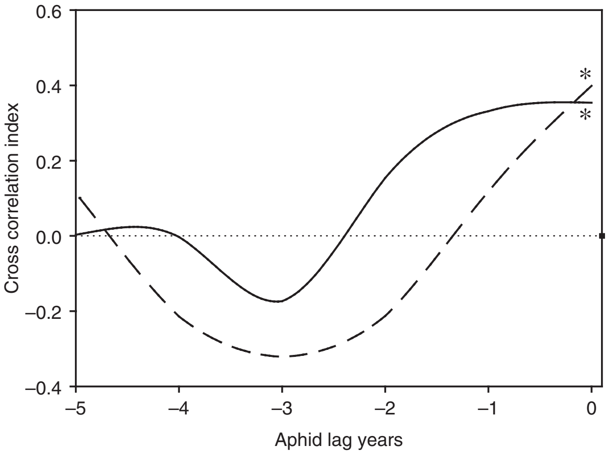

Fig. 3. A cross-correlation plot between *Sitobion avenae* and its parasitoids in aphid lag years at Rothamsted (-) and Writtle (--). An asterisk * indicates a *P*-value < 0.05 in that aphid lag year. The cross-correlation plot shows that only in the same year that parasitoids migrate are aphids significantly associated, and thus there are no lagged effects of aphids. Instead, the parasitoid–host relationship re-starts afresh each year.

In field systems over short time periods, it might be expected that there is a density-dependent effect of aphids on parasitoid communities (Hoover & Newman, 2004; Hance *et al.*, 2007). However, this does not necessarily hold for migration parasitoid–host dynamics. Cross-correlation analyses showed that there were no lagged year effects of aphids on parasitoid numbers (Fig. 3). Instead, statistically significant correlations were only found between parasitoids and *S. avenae* in the same year. As the lagged effect of aphids increased towards 5 years, a decay in the correlation coefficient after three lagged years was apparent and this coefficient later dissipated into a random relationship at lags 4–5 years. Importantly and unlike first flights of aphids (Bell *et al.*, 2015), the peak week is not steadily shifting forward with time either (Rothamsted: $\beta = -0.049 \pm$ SE 0.263, $t = -0.19$, $P = 0.852$. Writtle: $\beta = -0.021 \pm$ SE 0.184, $t = -0.12$; $P = 0.909$). Instead the peak week fluctuates widely according to temperature, as shown earlier.

In practice, marginal asynchrony in which the parasitoids arrive a few days before the aphid could favour better biological control if the pest arrives in enough numbers to support the awaiting parasitoid community. However, as Godfray *et al.* (1994) note, this early arrival strategy may have a destabilising force on the interaction because the few hosts that are present are subject to extreme parasitism risk that would lead to a low host population in the following year. It has been shown by van Nouhuys and Lei (2004) that the degree of synchrony varies considerably between years in a butterfly–parasitoid system. Despite this variation, there was no effect on host population size (van Nouhuys & Lei, 2004), suggesting that this system is tolerant to moderate asynchrony.

These preliminary data are the first to examine long-term migration patterns between parasitoids and their hosts. We have taken the initial steps to responding to the call by Jeffs and Lewis (2013) for data on migration and dispersal under climate change. We have examined the temporal synchrony between aphids and their parasitoids and found that more parasitoids migrated with increasing numbers of aphids. Further, we established that host–parasitoid migration peaks corresponded although there was no evidence that these peaks responded directly to temperature or were getting earlier over time. The temperature may not always explain differences in migration patterns but this should not be interpreted as meaning that temperature is irrelevant to migration, more that the threshold for flight was routinely exceeded during the peak summer migration. Instead, the likely mechanism that promotes migration peaks would appear to be through the plant, particularly in regard to the phenology of crop senescence, although we cannot formally test this owing to a lack of historical plant phenology data. There would be benefit in investigating the data in greater depth through quantification of the parasitoid–host relationship at all long-term monitoring suction-trap sites in the U.K. On this basis, the study would glean information from a total of 15 locations around the U.K., from northern Scotland to south-west England. There is the potential to examine the same across Europe, provided that suction-trap operators kept archived samples for parasitoid identification (Harrington *et al.*, 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12241

Figure S1. (a,b) Parasitoid species composition.

Table S1. Catch dates by site.

References

Bell, J.R., Alderson, L., Izera, D., Kruger, T., Parker, S., Pickup, J. *et al.* (2015) Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. *Journal of Animal Ecology*, **84**, 21–34.

Brewer, M.J. & Elliott, N.C. (2004) Biological control of cereal aphids in North America and mediating effects of host plant and habitat manipulations. *Annual Review of Entomology*, **49**, 219–242.

Brockhurst, M.A., Chapman, T., King, K.C., Mank, J.E., Paterson, S. & Hurst, G.D.D. (2014) Running with the Red Queen: the role of biotic conflicts in evolution. *Proceedings of the Royal Society B*, **281**, 20141382.

Chapman, J.W., Reynolds, D.R., Smith, A.D., Smith, E.T. & Woiwod, I.P. (2004) An aerial netting study of insects migrating at high-altitude over England. *Bulletin of Entomological Research*, **94**, 123–136.

Chua, T.H., González, D. & Bellows, T. (1990) Searching efficiency and multiparasitism in *Aphidius smithi* and *A. ervi* (Hym., Aphidiidae), parasites of pea aphid, *Acyrthosiphon pisum* (Hom., Aphididae). *Journal of Applied Entomology*, **110**, 101–106.

Dedryver, C.A., Le Ralec, A. & Fabre, F. (2010) The conflicting relationships between aphids and men: a review of aphid damages and control strategies. *Comptes Rendus Biologies*, **333**, 539–553.

Derocles, S.A., Plantegenest, M., Ait-Ighil, E.E.T., Chaubet, B., Dedryver, C.A. & Le Ralec, A. (2014) Larval hitch-hiking and adult flight are two ways of Aphidiinae parasitoids long-range dispersal. *Environmental Entomology*, **43**, 1327–1332.

Dixon, A.F.G. (1987) Cereal aphids as an applied problem. *Agricultural Zoology Reviews*, **2**, 1–57.

Ekbom, B.S., Wiktelius, S. & Chiverton, P.A. (1992) Can polyphagous predators control the bird cherry-oat aphid (*Rhopalosiphum padi*) in spring cereals?: A simulation study. *Entomologia Experimentalis et Applicata*, **65**, 215–223.

FAO (2014) *FAO Cereal Supply and Demand Brief* [WWW document]. URL http://www.fao.org/worldfoodsituation/csdb/en/ [accessed on 18 June 2014].

Foster, S.P., Paul, V.L., Slater, R., Warren, A., Denholm, I., Field, L.M. *et al.* (2014) A mutation (L1014F) in the voltage-gated sodium channel of the grain aphid, *Sitobion avenae*, is associated with resistance to pyrethroid insecticides. *Pest Management Science*, **70**, 1249–1253.

Godfray, H.C.J., Hassell, M.P. & Holt, R.D. (1994) The dynamic consequences of the disruption of synchrony between hosts and parasitoids. *Journal of Animal Ecology*, **63**, 1–10.

Hance, T., van Baaren, J., Vernon, P. & Boivin, G. (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology*, **52**, 107–126.

Harrington, R., Clark, S.J., Welham, S.J., Verrier, P.J., Denholm, C.H., Hullé, M. *et al.* (2007) Environmental change and the phenology of European aphids. *Global Change Biology*, **13**, 1550–1564.

Höller, C., Borgemeister, C., Haardt, H. & Powell, W. (1993) The relationship between primary parasitoids and hyperparasitoids of cereal aphids: an analysis of field data. *Journal of Animal Ecology*, **62**, 12–21.

Hoover, J.K. & Newman, J.A. (2004) Tritrophic interactions in the context of climate change: a model of grasses, cereal aphids and their parasitoids. *Global Change Biology*, **10**, 1197–1208.

Huang, Z.H., Feng, M.G., Chen, X.X. & Liu, S.S. (2008) Pathogenic fungi and parasitoids of aphids present in air captures of migratory alates in the low-latitude plateau of Yunnan, China. *Environmental Entomology*, **37**, 1264–1271.

Jeffs, C.T. & Lewis, O.T. (2013) Effects of climate warming on host–parasitoid interactions. *Ecological Entomology*, **38**, 209–218.

Klapwijk, M.J., Groebler, B.C., Ward, K., Wheeler, D. & Lewis, O.T. (2010) Influence of experimental warming and shading on host–parasitoid synchrony. *Global Change Biology*, **16**, 102–112.

Langer, A., Boivin, G. & Hance, T. (2004) Oviposition, flight and walking capacity at low temperatures of four aphid parasitoid species (Hymenoptera: Aphidiinae). *European Journal of Entomology*, **101**, 473–480.

Macaulay, E.D.M., Tatchell, G.M. & Taylor, L.R. (1988) The Rothamsted Insect Survey ‘12-metre’ suction trap. *Bulletin of Entomological Research*, **78**, 121–128.

Macfadyen, S., Gibson, R., Raso, L., Sint, D., Traugott, M. & Memmott, J. (2009) Parasitoid control of aphids in organic and conventional farming systems. *Agriculture Ecosystems and Environment*, **133**, 14–18.

Meiners, T. & Peri, E. (2013) Chemical ecology of insect parasitoids: essential elements for developing effective biological control programmes. *Chemical Ecology of Insect Parasitoids* (ed. by E. Wajnberg and S. Colazza), 193–224. John Wiley & Sons, Ltd, Chichester, U.K.

van Nouhuys, S. & Lei, G. (2004) Parasitoid–host metapopulation dynamics: the causes and consequences of phenological asynchrony. *Journal of Animal Ecology*, **73**, 526–535.

Powell, W. (1982) The identification of hymenopterous parasitoids attacking cereal aphids in Britain. *Systematic Entomology*, **7**, 465–473.

Rafferty, N.E., CaraDonna, P.J., Burkle, L.A., Iler, A.M. & Bronstein, J.L. (2013) Phenological overlap of interacting species in a changing climate: an assessment of available approaches. *Ecology and Evolution*, **3**, 3183–3193.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Schellhorn, N.A., Bianchi, F.J.J.A. & Hsu, C.L. (2014) Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. *Annual Review of Entomology*, **59**, 559–581.

Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. & Tscharntke, T. (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of London B*, **270**, 1905–1909.

Stary, P. (1970) *Biology of Aphid Parasites (Hymenoptera: Aphidiidae) with Respect to Integrated Control. Series Entomologica*, Vol. 6. DR. W. Junk, The Hague, The Netherlands.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R. *et al.* (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304–3313.

Traugott, M., Bell, J.R., Broad, G.R., Powell, W., Van Veen, J.F., Vollhardt, I.M.G. *et al.* (2008) Endoparasitism in cereal aphids: molecular analysis of a whole parasitoid community. *Molecular Ecology*, **17**, 3928–3938.

Traugott, M., Bell, J.R., Raso, L., Sint, D. & Symondson, W.O.C. (2012) Generalist predators disrupt parasitoid aphid control by direct and coincidental intraguild predation. *Bulletin of Entomological Research*, **102**, 239–247.

Van Valen, L. (1973) A new evolutionary law. *Evolutionary Theory*, **1**, 1–30.

Vickerman, G.P. & Wratten, S.D. (1979) The biology and pest status of cereal aphids (Hemiptera: Aphididae) in Europe: a review. *Bulletin of Entomological Research*, **69**, 1–32.

Walton, M.P., Powell, W., Loxdale, H.D. & Allen-Williams, L. (1990) Electrophoresis as a tool for estimating levels of hymenopterous parasitism in field populations of the cereal aphid. *Entomologia Experimentalis et Applicata*, **54**, 271–279.

Walton, M.P., Loxdale, H.D. & Allen-Williams, L. (2011) Flying with a ‘death sentence’ on board: electrophoretic detection of braconid parasitoid larvae in migrating winged grain aphids, *Sitobion avenae* (F.). *Bulletin of Entomological Research*, **101**, 443–449.

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