RESEARCH ARTICLE

Longer photoperiods through range shifts and artificial light lead to a destabilizing increase in host–parasitoid interaction strength

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Abstract

1. Many organisms are experiencing changing daily light regimes due to latitudinal range shifts driven by climate change and increased artificial light at night (ALAN). Activity patterns are often driven by light cycles, which will have important consequences for species interactions.

2. We tested whether longer photoperiods lead to higher parasitism rates by a day-active parasitoid on its host using a laboratory experiment in which we independently varied daylength and the presence of ALAN. We then tested whether reduced nighttime temperature tempers the effect of ALAN.

3. We found that parasitism rate increased with daylength, with ALAN intensifying this effect only when the temperature was not reduced at night. The impact of ALAN was more pronounced under short daylength. Increased parasitoid activity was not compensated for by reduced life span, indicating that increased daylength leads to an increase in total parasitism effects on fitness.

4. To test the significance of increased parasitism rate for population dynamics, we developed a host–parasitoid model. The results of the model predicted an increase in time-to-equilibrium with increased daylength and, crucially, a threshold daylength above which interactions are unstable, leading to local extinctions.

5. Here we demonstrate that ALAN impact interacts with daylength and temperature by changing the interaction strength between a common day-active consumer species and its host in a predictable way. Our results further suggest that range expansion or ALAN-induced changes in light regimes experienced by insects and their natural enemies will result in unstable dynamics beyond key tipping points in daylength.

KEYWORDS
aphid, climate change, interaction, light pollution, parasitoid, photoperiod, range expansion, stability

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1 | INTRODUCTION

Climate change has caused many species to shift their ranges poleward (Parmesan & Yohe, 2003), altering their interactions with other species (Carrasco et al., 2018; Ettinger & HilleRisLambers, 2017). However, as species track their thermal niches, and move closer to the poles, they experience longer summer days. Additionally, the light cycles they experience throughout their range are now less predictable due to the increasingly widespread introduction and increased use of artificial light at night (ALAN). Much of this lighting has also become brighter and with a broader spectral range than in the 20th century (Elvidge, Keith, Tuttle, & Baugh, 2010; Gaston, Duffy, Gaston, Bennie, & Davies, 2014; Kyba et al., 2017). Approximately 23% of global land area now experiences light pollution (Falchi et al., 2016). ALAN causes a range of biological effects, such as advancing budburst timings by 7 days (Ffrench-Constant et al., 2016; Partanen, Koski, & Hänninen, 1998) and altering activity patterns (e.g. Beier, 2006; Stone, Jones, & Harris, 2009).

Given that daily light cycles govern the activity patterns of many insect species, such changes in light regime are likely to affect the direct and indirect interactions among insect species. One key, and agriculturally important, species interaction is between European aphids and their parasitoids. A multi-generational experiment has shown that increasing the daylength experienced by an aphid–parasitoid community altered the relative abundance of the aphid species (Kehoe, Cruse, Sanders, Gaston, & van Veen, 2018). ALAN also affects the dynamics of such systems, destabilizing communities (Sanders, Kehoe, Cruse, van Veen, & Gaston, 2018; Sanders et al., 2015). A potential mechanism for these effects is an increase in parasitoid daily activity with increased photoperiod (Guo, Snell, & Yang, 2010; Zilahi-Balogh, Shipp, Cloutier, & Brodeur, 2006), leading to higher attack rates. It is, therefore, becoming clear that predicting some of the effects of global change depends on understanding the effect of altered photoperiod and ALAN on species' interactions, in concert with its direct effects on species' performance (Sanders, Kehoe, et al., 2018; Sanders et al., 2016; Urban et al., 2016). Furthermore, any short-term effects on interactions, as measured in experiments, should be incorporated in population-dynamic models to better understand and predict their potential long-term population-level consequences, which may include not only changes in equilibrium densities but also in stability and thereby population fluctuations and outbreaks (van Veen, van Holland, & Godfray, 2005).

The responses of agricultural pests to climate change and how they interact with responses to other forms of anthropogenic change such as ALAN remain a key unknown in predicting crop productivity under future climates (Gornall et al., 2010). Aphids and their natural enemies are an important model system to address this question, given the detailed understanding of their life history and ecology, and because many species are major agricultural pests, causing extensive damage to crops (Dedryver, Le Ralec, & Fabre, 2010). Parasitoid wasps are an important group of natural enemies of aphids and are widely used as biological control agents in agriculture (van Veen, Müller, Pell, & Godfray, 2008; von Burg, van Veen, Álvarez-Alfageme, & Romeis, 2011). They are mainly active during daylight

hours (Sanders, Kehoe, et al., 2018). Therefore, if their host parasitism rate is time-limited (Henri, Seager, Weller, & van Veen, 2012), parasitism rates should increase with longer daily light exposure, whether from longer daylength or ALAN. ALAN has the potential to increase activity, but for ectothermic animals (whose activity is also reliant on temperature), this will only be possible when nighttime temperatures also permit activity. However, any effect of increased attack rate on population dynamics could reduce if it is associated with a reduction in the reproductive life span (and attack rate later in life) of parasitoids, in the manner of 'live fast, die young' (Travers, Garcia-Gonzalez, & Simmons, 2015). This effect would reduce any effect on increased lifetime fecundity of the parasitoids.

In this study, we use controlled experiments to test the following predictions of the effect of photoperiod on parasitism rate: (1) Longer daylengths lead to higher daily parasitism rates of parasitoids on aphids; (2) Exposure to ALAN is associated with higher parasitism rates; (3) Reduced nighttime temperature relative to daytime reduces the effect of ALAN on parasitism rates; (4) ALAN impact will be stronger under shorter daylength. (5) Increased parasitoid attacks associated with long day treatments in early life will reduce attack frequency later in life so that lifetime fecundity remains unaffected by photoperiod. Finally, we apply the effects we observe in predictions 1–5 above to a host–parasitoid population dynamic model. This model allows us to predict (6) the effects of photoperiod on the stability of host–parasitoid interactions and thereby the likelihood of light regime-driven extinctions and pest outbreaks in a range of biologically and environmentally realistic parameters.

2 | MATERIALS AND METHODS

2.1 | Study system

We used a plant–aphid–parasitoid food chain consisting of broad bean plants (*Vicia faba*, L., var. the Sutton, grown from seed) as the food resource for the vetch aphid *Megoura viciae* (Buckton). *Megoura viciae*, in turn, was the host of the day-active parasitoid *Aphidius megourae* (Stary).

2.2 | Experiment 1: Impact of daylength, ALAN and night temperature on parasitism rate

To assess how different day–night regimes, artificial light and a reduction in nighttime temperature affect the parasitism rate of the parasitoid *A. megourae*, we conducted a laboratory experiment where individual parasitoids were exposed to 100 aphids under one of 16 treatments for 24 hr. This short-term experiment recreates the first generation of a parasitoid which has recently expanded its range through range expansion or migration. Each experimental trial consisted of a 2-week-old broad bean plant infected with 100 third instar *Megoura viciae* aphids (100 aphids is above the maximum number that can be attacked within 24 hr by *A. megourae* ; Sanders, Kehoe, et al., 2018). We then covered each plant with a ventilated, transparent plastic bag for the duration of

the experiment. A freshly hatched (<12 hr old) mated female *A. megourae* parasitoid, from stock culture, reared at a 16:8 L:D regime at 18°C was then released onto the plant, and the replicate placed into a climate chamber (Percival Model 1-30vl).

Once in the climate chambers, each plant was exposed to one of the 16 experimental treatments, in a fully cross-factored design that consisted of four different daylength treatments (12:12, 14:10, 16:8 and 18:6 hr day-night cycles). The day–time light was set to 4,239 lux, equivalent to a typical overcast day (Gaston, Bennie, Davies, & Hopkins, 2013). For each daylength treatment, half of the mesocosms were exposed to completely dark nights, while the other half experienced artificial light during the night period (20 lux, equivalent to street lighting; Gaston et al., 2013; Stone et al., 2009). These treatments were further divided into those exposed to constant temperature (18°C) or exposed to a drop in nighttime temperatures (18°C during the day and 12°C at night) to simulate the natural drop (see Table S1 for a summary). Each treatment was replicated 10 times, giving a total of 160 plant–aphid–parasitoid trials.

Each replicate was left in the climate chamber for 24 hr, after which time the parasitoid was removed, and the plants relocated to a temperature-controlled room set to 16:8 light:dark and 18°C and were left for 2 weeks. The bag was then removed, and the number of aphid mummies (indicating the number of successful attacks) counted.

2.3 | Experiment 2: Impact of daylength on parasitoid longevity and lifetime fecundity

A freshly hatched (<12 hr old) mated female *A. megourae* parasitoid, from stock culture, reared at a 16:8 L:D regime at 18°C was placed in a transparent ventilated plastic bag with one 2-week-old broad bean plant, and 100 third instar *M. viciae* aphids. This mesocosm was then placed in a climate chamber set to either 12:12 or 18:6 hr light:dark and constant 18°C temperature. Each day at noon the parasitoid was removed from the mesocosm and placed in a new one with 100 new aphids on a new plant. This daily transfer continued until the death of the parasitoid. Once the parasitoid was removed from each mesocosm and placed in the new one, the old mesocosm, complete with bean plant and both parasitized and unparasitized aphids, was placed in an 18°C controlled temperature room at 16:8 light:dark for 2 weeks to allow the mummies to develop. The number of mummies, signifying the number of successful attacks, was then recorded. Each treatment was replicated seven times, giving a total of 14 parasitoids.

2.4 | Statistical analysis

2.4.1 | Experiment 1

To analyse the number of successful attacks by *A. megourae*, we used a generalized linear model with a quasibinomial error structure. The proportion of aphids that were successfully parasitized was used as the response variable, and a three-way interaction between daylength, ALAN and a reduction in night temperature included into the model as the explanatory variables. Daylength was analysed as a continuous variable.

2.4.2 | Experiment 2

The lifetime fecundity of *A. megourae* was analysed using a mixed-effects model from the package *nlme* (Pinheiro et al., 2017), with the number of mummies as the response variable, and daylength and day as explanatory variables. The terms 'parasitoid ID' and 'Day' which represents parasitoid age over the time of the experiment were used as random effects. The significance of the interaction between parasitoid age and daylength was also tested by comparing the model with and without the interaction using likelihood ratio tests. Temporal autocorrelation was negligible (all partial autocorrelations were below 0.2), and therefore not included in the model. Model assumptions were checked visually for heteroscedasticity and common distributions.

We performed all analyses using R version 3.5.1 (R Core Team, 2018). Final models were chosen based on the lowest AIC values (Akaike, 1998) and by using likelihood ratio tests to determine which parameters were included.

2.5 | Testing the effect of changes in parasitism rate on population dynamics models

To assess how any changes in parasitism rate of *A. megourae* with increasing light hours, as observed in the experiments, would affect the population dynamics of its interaction with *M. viciae*, we used a variation of the Lotka–Volterra predator–prey model, specifically modified and parameterized for aphid–parasitoid systems (van Veen et al., 2005).

$$\frac{dN}{dt} = rN(1 - \alpha N) - N\frac{\alpha_P P}{1 + bN},$$

$$\frac{dP}{dt} = N\frac{s\alpha_P P}{1 + bN + cP} - \mu P.$$

This model describes the relationship between a host (N) and a parasitoid (P). Here, r represents the intrinsic rate of aphid increase and α the intraspecific competition coefficient for the host (i.e. the inverse of their carrying capacity). Parasitoid handling time is represented by b, parasitoid attack rate by α_p and parasitoid sex ratio by s. The effect of parasitoid density on its recruitment is represented by c, and parasitoids die at a density-independent rate of μ.

System-specific parameter values were estimated from the dynamics of experimental populations by van Veen et al. (2005) as $r = 3.22$, $b = 0.0233$, $s = 0.5$, $c = 1.26$, $\mu = 0.634$, $\alpha_p = 0.281$ (at 16 hr daylight). Here, to generate predictions for a wider range of potential species, we created 1,000 sets of parameter values for r, b and μ by randomly sampling these from normal distributions with the estimated values above as the mean and a standard deviation of the mean divided by 20. Values for s and c were fixed at the above estimates. We set the host carrying capacity at an arbitrary value of 10,000, which corresponds to $\alpha = 0.0001$.

To simulate the effect of daylength, we assume that parasitoid attack rate is proportional to the number of daylight hours. This is the most parsimonious assumption for time-limited parasitoids attacking hosts at a constant rate during a daily active period that is limited by photoperiod. Based on the estimated value of $\alpha_p = 0.28$ at a daylength of 16 hr in van Veen et al. (2005), we used a range of α_p of 0.21–0.32 to correspond with daylengths ranging from 12 to 18 hr. For each of the 1,000 sets of randomly selected parameter values we ran the model for this range of α_p, in increments of 0.01, thus for a total of 12,000 sets of parameter values.

Using the function 'ode' in R-package DeSolve (Soetaert, Petzoldt, & Setzer, 2010), we created numerical solutions for the model for 100 time steps (1 time step corresponds to 1 week or half a generation time with these parameter values; van Veen et al., 2005) with a host starting density at carrying capacity and parasitoid starting density set at 1. Thus we simulate a parasitoid population invading a stable host population. Invariably this results in initial fluctuations in population density for both species that, depending on parameter values, either diminish over time until new equilibrium densities are reached or that continue indefinitely, typically in a diverging fashion (latter cases would realistically lead to extinctions). For each of the 12,000 sets of parameter values, we recorded whether the populations reached a stable equilibrium and, if so, the aphid and parasitoid densities at equilibrium, and the time taken to reach the equilibrium (defined as the first point where the densities of both host and parasitoid populations are within 0.0001 from the previous two time points) and plotted these values against the value of α_p.

3 | RESULTS

3.1 | Experiment 1: Impact of daylength, ALAN and night temperature on parasitism rate

The duration of light hours per day had a marked impact on parasitoid performance. We found a significant three-way interaction between daylength, ALAN and a reduction in night temperature on the parasitism rate of *A. megourae* ($t_{152} = -2.627$, $p < 0.01$; Table 1;

Figure 1a). This interaction indicated that all three variables and their interactions were important in explaining the parasitoid's response to changes in light regime. Overall, longer daylight hours were associated with an increased mean parasitism rate of *A. megourae* from 31.48 ± 15.58 *SD* successful attacks out of 100 aphids at 12-hr days to 61.26 ± 17.12 at 18-hr days (Figure 1a; Table 1).
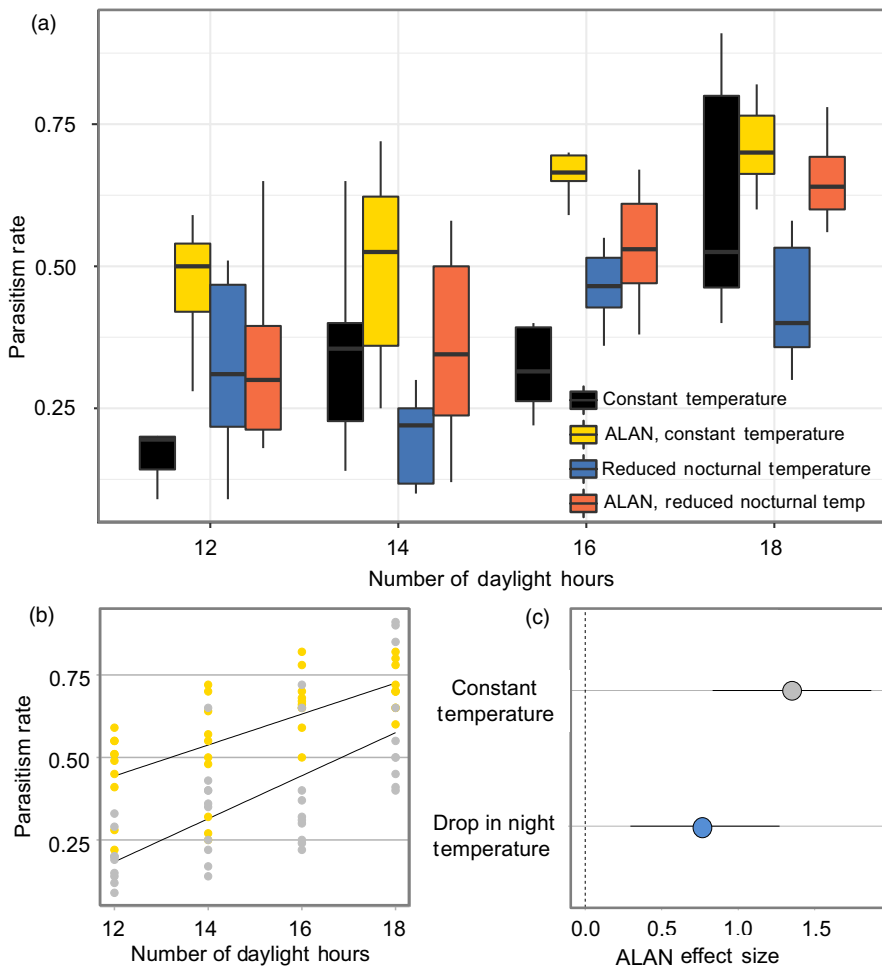
Additionally, parasitoids experiencing ALAN under constant temperature increased their parasitism rate by an average of 26.5 per 100 aphids at short daylight hours. This effect diminished at a high number of daylight hours to an average increase of 10 per 100 aphids, such that the slope of the relationship between daylength and parasitism rate was shallower in the presence of ALAN (Figure 1b). However, this effect of ALAN on parasitism rate was weaker if it was associated with a drop in night temperature (Figure 1c; Table 1).

## 3.2 | Experiment 2: Impact of daylength on lifetime fecundity

A longer photoperiod increased the overall fecundity of *A. megourae*, from 82 ± 36.66 *SD* successful parasitization events over a parasitoid's lifetime at a daylength of 12 hr to 132.67 ± 55.84 at a daylength of 18 hr ($t_{28} = 3.5$, $p = 0.002$; Figure 2b). In addition, parasitism rate decreased with age from 0.23 ± 0.09 (12:12) and 0.41 ± 0.01 (18:06) at the first day to 0.05 ± 0.007 (12:12) and 0.05 ± 0.008 (18:06) on day 7 ($t_{40} = -7.3$, $p \leq 0.001$; Figure 2). There was no interaction between photoperiod and parasitoid age ($\chi^2 = 1.6$, $df = 1$, $p = 0.2$), showing that the effect of daylength was consistent over the lifetime of the parasitoids, with no apparent cost of increased reproduction in early life on reproduction at later stages. There was also no significant effect of daylength treatment on survival of parasitoids (Figure S1).

3.3 | Impact of parasitism rate on population dynamic models

At lower levels of parasitism rate the majority of simulations show damped oscillations leading to a stable equilibrium but time taken to

TABLE 1 Results of a generalized linear model with quasibinomial error structure, including a three-way interaction between daylength, ALAN and a drop in night temperature on *Aphidius megourae*'s parasitism rate. Levels of significance: **$p < 0.01$; ***$p < 0.001$. Bold values indicate significance of $p < 0.05$

	Estimate	SE	df	t Value	p Value
Intercept	2.68	0.34	159	−5.28	**<0.001***
Daylength	0.09	0.02	158	3.73	**0.001***
ALAN	−1.96	0.53	157	−3.65	**0.001***
Drop in night temperature	−1.04	0.50	156	−1.83	0.07
Daylength × ALAN	0.09	0.03	155	2.84	**0.005**
Daylength × Drop in night temperature	0.05	0.03	154	1.41	0.16
ALAN × Drop in night temperature	2.09	0.76	153	2.86	**0.005**
Daylength × ALAN × Drop in night temperature	−0.12	0.05	152	−2.63	**0.009**

Abbreviation: ALAN, artificial light at night.

FIGURE 1 Parasitism rate as a measure of interaction strength. (a) Boxplots with median, and quartiles showing the effect of all treatments (daylength, artificial light at night and a reduction in temperature at night) on the parasitism rate of *Aphidius megourae* on 100 *Megoura viciae* aphids over a 24-hr period. (b) Line plot showing individual values, mean and 95% CI based on a linear model for each daylength incorporating unlit and lit treatments without a drop in temperature. (c) The effect size (standardized mean difference) of ALAN on the parasitism rate of *A. megourae* under a drop in night versus day temperature compared to constant temperature treatments
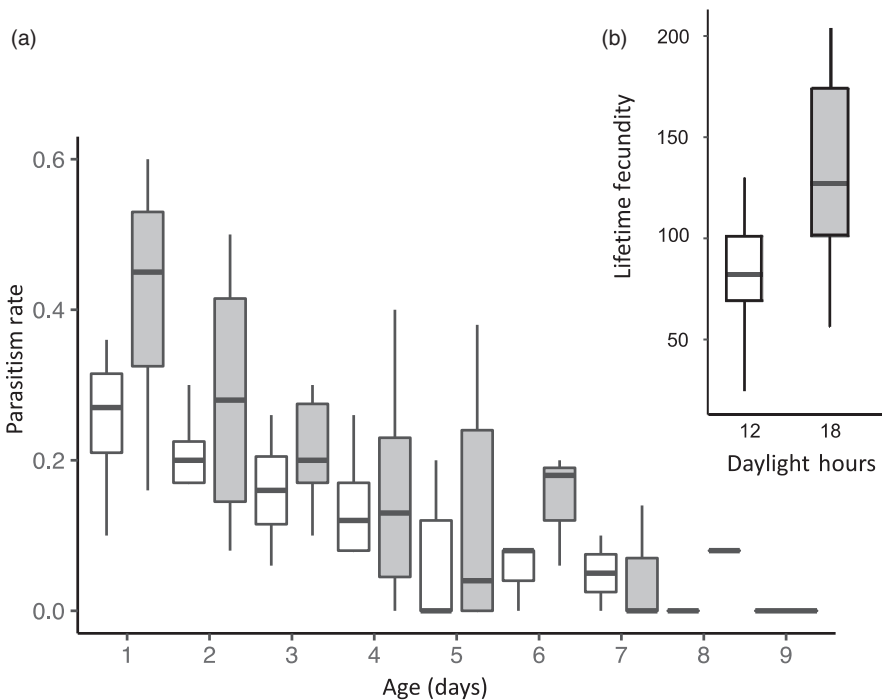
FIGURE 2 (a) Box plot and interquartile range showing the effect of daylength on the parasitism rate of *Aphidius megourae* over the parasitoids' lifetime. White boxes display the 12-hr daylength treatment and grey boxes the 18-hr treatment. (b) shows overall lifetime fecundity as the sum of all successful attacks

FIGURE 3 The median and interquartile range of the time for the Lotka–Volterra model to reach equilibrium, based on 1,000 simulations per attack rate step, loess regression (orange line) and proportion of simulations reaching equilibrium (dark red line) (a). The median and interquartile range for population densities of parasitoids (b) and aphids (c) and at the point of equilibrium
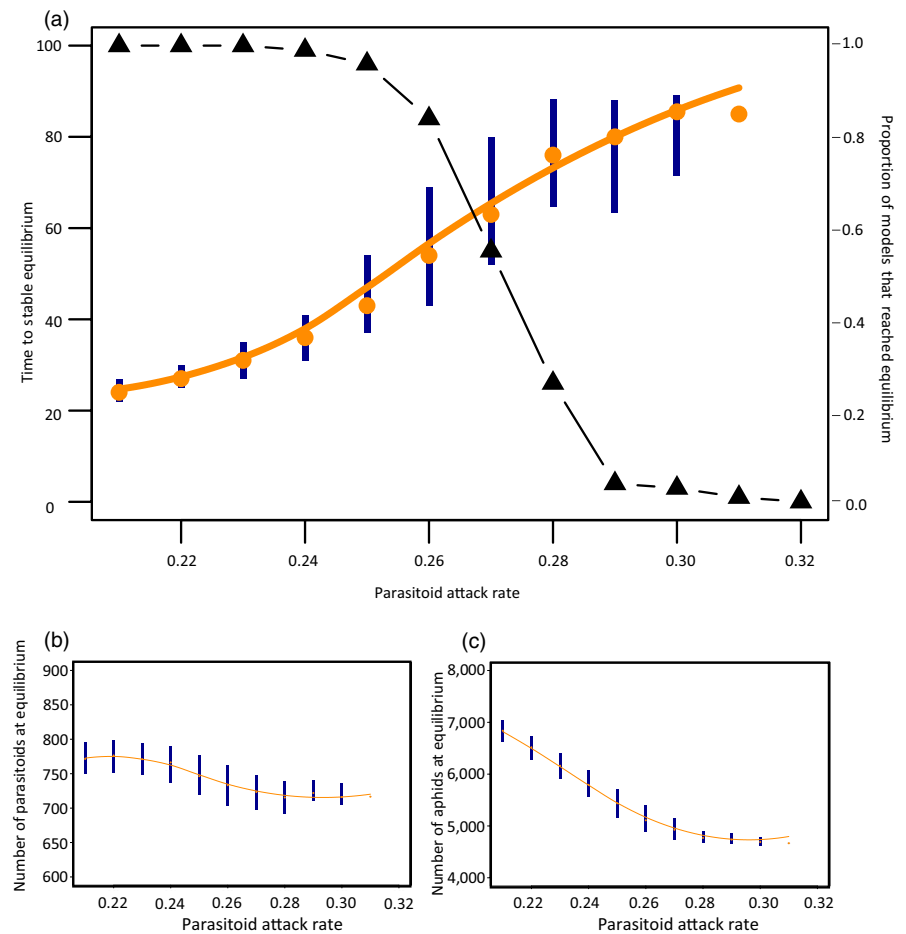
reach equilibrium increases with higher attack rates while the proportion reaching an equilibrium declines rapidly (Figure 3a). Focusing on only those sets of parameters where an equilibrium is reached, the equilibrium densities of the parasitoid and especially the host decrease with increasing attack rate (Figure 3b,c). In these scenarios, the equilibrium density of the host decreased with increasing attack rate. The remaining simulations did not reach an equilibrium instead showing indefinite wide fluctuations, which in reality would no doubt lead to (local) population extinctions.

4 | DISCUSSION

Our experiments test the relationship between interaction strength and light regime for a common diurnal consumer species and its host. The results demonstrate that the strength of the interaction between the parasitoid *A. megourae* and its host *M. viciae* depends closely on light regimes, with both increasing daylength and artificial light at night increasing the parasitism rate of *A. megourae*. There was a steep increase in parasitism rate with longer daylength, which was matched by a positive effect of ALAN on parasitism rate that was strongest under shorter daylengths. However, this increase in parasitism rates associated with ALAN was weaker when there was a nocturnal drop in temperature of 6°C (i.e. cool nights and warmer days, as is typically the case in temperate regions), indicating that the effect of ALAN

might be limited by nighttime temperatures. Further, in our second experiment we showed that these effects are sustained over a parasitoid's life and can therefore be expected to affect the host–parasitoid interaction strength and thereby population dynamics. Our modelling results do indeed lead us to predict that host–parasitoid dynamics are altered by increased daylength such that stable equilibria become less likely and take longer to be reached from non-equilibrium starting points. These results highlight how increased parasitoid activity periods, due to poleward range shifts and/or ALAN, can have substantial effects on host–parasitoid dynamics.

It has previously been shown that both an increase in temperature and the presence of artificial light can increase parasitism rate in some parasitoids (Burnett, 1951; Malina & Praslicka, 2008), but not in others (Heimpel & Rosenheim, 1998). Here we show how ALAN, nighttime temperature and daylength interact in driving parasitism rate. In the absence of ALAN, a drop in nighttime temperature had little or no effect on parasitism rate in our study, probably because day-active parasitoids are not active when it is dark, irrespective of temperature (Sanders, Kehoe, et al., 2018). However, under ALAN, nighttime temperature becomes the limiting factor determining the activity level of the parasitoid. Here, we only included two nocturnal temperature treatments, and so cannot detect any nonlinearity or threshold effects in this relationship.

The interaction observed between daylength and ALAN, where the effect of the latter was most pronounced under short days,

highlights that the effect of ALAN on species and their communities may depend on the season and associated day–night regimes. Our results suggest that ALAN will increase parasitism rates more in early spring and autumn when natural daylength is shorter, but only in situations where nighttime temperature is not a limiting factor. The effect of ALAN will also be more likely in more southerly latitudes during the summer where days are shorter and nights warmer. We may also expect stronger effects in urban environments where high prevalence of ALAN is associated with raised nighttime temperatures due to the urban heat island effect (Nichol, 2005). Given that nighttime temperatures are known to be increasing at rates greater than daytime temperatures due to climate change (Davy, Esau, Chernokulsky, Outten, & Zilitinkevich, 2017), this impact of ALAN on populations is likely to increase with ongoing climate change.

The observation of increased parasitism under long daylengths indicates that these day-active parasitoids are time- rather than egg-limited. However, one might expect that increased oviposition opportunities, due to longer active periods, come at a cost in terms of reduced fecundity or survival later in life, as finite resources are used up more rapidly (Ellers & Van Alphen, 1997). As such, the effect of increased daily activity periods in early life could be cancelled out in later life to leave the cumulative number of hosts killed by a parasitoid over its lifetime unaffected. Our second experiment, however, could not detect such a trade-off between early and late life as lifetime fecundity of parasitoids was significantly higher at longer days (Figure 2b) and survival was not affected by daylength. Furthermore, in natural habitats, parasitoid life span is likely to be much shorter than in the laboratory due to elevated extrinsic mortality rates. As such, the effects of daylength on parasitism rate in early life reported here are probably the most representative measure. These early life rates of parasitism and their sensitivity to light and temperature constraints on the length of the daily activity period are therefore likely to have a major effect on species interactions in natural populations.

The observed effect of photoperiod on parasitism rate implies a similar effect on host–parasitoid interaction strength, which is a critical parameter determining population dynamics. With our model, we tested how the daylength-associated changes in parasitism rate that we observed empirically, are likely to affect host–parasitoid population dynamics. In this modified Lotka–Volterra model, the interaction strength between host and parasitoid is represented by the attack rate parameter which is related, but not identical, to the daily parasitism rate that we measured in our experiments. We assumed that attack rate is proportional to the length of the daily activity period (i.e. daylength), using the estimate for attack rate at a 16-hr daylength (van Veen et al., 2005) to give us a representative range for daylengths of 12–18 hr. This simple linear relationship between daylength and attack rate is the most parsimonious approach and is further justified by our experimental results, which show a linear relationship between daylength and parasitism rate in our first experiment, and a similar ratio of lifetime fecundity (i.e. cumulative number of hosts killed) to daylight hours in the 12- and 18-hr daylength treatments of our second experiment. It is of course possible that this relationship becomes shallower if it were to be

extended to longer days but, given that our results show that dynamics are predicted to be invariably highly unstable at longer days (as discussed below), the exact relationship between daylength and attack rate at these extremes is largely irrelevant.

Our model results showed that with increasing attack rate equilibrium host density declines and the population dynamics become less stable (measured as the proportion of the 1,000 sets of parameter values for which the model populations reach a stable equilibrium and as the time taken to reach that equilibrium, given the starting densities). When the attack rate parameter is ≥0.28 (equivalent to daylengths >16 hr) almost none of the parameter sets lead to a stable equilibrium (Figure 3) and the dynamics are largely chaotic in nature, with irregularly spaced high amplitude fluctuations. In nature, one would expect this to lead to a high frequency of local extinctions as well as large outbreaks, unless other stabilizing factors prevent this (e.g. Kehoe et al., 2016; Sanders, Thébault, Kehoe, & Van Veen, 2018). Importantly, this means for crop pest insects controlled by parasitoids, or similarly day-active and time-limited natural enemies, that although equilibrium pest densities will initially decline with poleward range-shifts, the population fluctuations will also increase and potentially dramatically so. This increased variation may result in more unpredictable and damaging pest outbreaks. Our model predicts that for any given set of species-specific parameter values, there is a threshold attack rate, and therefore latitude, above which there is no stable equilibrium. Additionally, the approach towards such a threshold would be characterized by a steadily decreasing prey abundance, but with increasing population fluctuations, as indicated by the increase in time-to-equilibrium.

In order to investigate the general principles, we kept daylength constant for each iteration of our model. However, daylength varies seasonally, and more strongly so nearer to the poles. Most temperate insects are only active between the spring and autumn equinoxes and daylengths at the start and end of the season will therefore be near 12 hr, irrespective of latitude, with a midsummer peak in daylength that increases with latitude. Our results should therefore not be considered predictions of at which precise latitudes the strong destabilizing effects will occur and more detailed investigations are required to study the effect of seasonal variation in daylength in this context. The species-specific number of generations per season and their timing will be important factors in this respect.

The experiments and modelling in this study demonstrate the potential importance of including natural and artificial light regimes when predicting the effects of environmental change on species interactions that determine the dynamics of ecological communities. Such understanding is especially important where food security depends on the natural control of agricultural pests. A vital next step is to test the model predictions of the effect of daylength on host–parasitoid dynamics experimentally. Finally, the strong response of a diurnal host–parasitoid system reported here also emphasizes the importance of focussing on the impact of ALAN not just on nocturnal species but also on those that are chiefly diurnal, on which the effects of ALAN may be just as profound, if not as intuitive.

AUTHORS' CONTRIBUTIONS

R.K., D.S. and F.v.V. conceived the ideas and designed methodology; R.K., M.S. and D.C. collected the data; R.K. and D.S. analysed the data; R.K. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are stored with figshare https://doi.org/10.6084/m9.figshare.12674528.v1 (Kehoe et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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