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The long-term population dynamics of common wasps in their native and invaded range

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Summary

1. Populations of introduced species are often thought to perform differently, or experience different population dynamics, in their introduced range compared to their native habitat. Differences between habitats in climate, competition or natural enemies may result in populations with varying density dependence and population dynamics.

2. We examined the long-term population dynamics of the invasive common wasp, *Vespula vulgaris*, in its native range in England and its invaded range in New Zealand. We used 39 years of wasp density data from four sites in England, and 23 years of data from six sites in New Zealand. Wasp population time series was examined using partial rate correlation functions. Gompertz population models and multivariate autoregressive state-space (MARSS) models were fitted, incorporating climatic variation.

3. Gompertz models successfully explained 59–66% of the variation in wasp abundance between years. Density dependence in wasp populations appeared to act similarly in both the native and invaded range, with wasp abundance in the previous year as the most important variable in predicting intrinsic rate of increase (r). No evidence of cyclic population dynamics was observed.

4. Both the Gompertz and MARSS models highlighted the role of weather conditions in each country as significant predictors of annual wasp abundance. The temporal evolution of wasp populations at all sites was best modelled jointly using a single latent dynamic factor for local trends, with the inclusion of a latent spring weather covariate. That same parsimonious multivariate model structure was optimal in both the native and invaded range.

5. Density dependence is overwhelmingly important in predicting wasp densities and ‘wasp years’ in both the native and invaded range. Spring weather conditions in both countries have a major influence, probably through their impact on wasp colony initiation and early development. The population dynamics in the native range and invaded range show no evidence of cyclic boom-and-bust dynamics. Invasive species may not exhibit different population dynamics despite considerable variation in abundances throughout their distribution.

Key-words: density dependence, invasive species, population dynamics, population regulation, time-series analysis, *Vespula vulgaris*

Introduction

Invasive species are often more abundant, more fecund and are typically larger in their introduced range (Parker *et al.* 2013). They are thought to experience enhanced niche opportunities in their invaded range, perhaps

through a greater availability of higher quality resources within habitats, release from natural enemy regulation, less exposure to extreme weather events, or some combination of these processes (MacLeod *et al.* 2009). Long time-series spanning many decades are required to help understand the factors that drive differences in population dynamics between the native and invaded range. There are, however, a lack of comparative data and analyses on the population dynamics of the majority of species,

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including those considered to be the world's most damaging invasive organisms (Parker *et al.* 2013; Frederiksen *et al.* 2014). Here, we examine the long-term population dynamics of one of the world's most damaging invasive insects: the common wasp *Vespula vulgaris* (L.).

The question of why populations fluctuate is fundamental for the management of populations towards conservation or pest control goals (Royama 1992; Berryman 1999; Turchin 1999). Variation in population densities over time may be a result of exogenous factors such as climatic variation, or endogenous (density dependent) effects. A key question is if there is evidence of first-order density dependence, and/or higher order or delayed density-dependent effects. To generate population cycles second-order (or higher) lags are needed. Higher order density dependence can be indicative of disease, food supplies or predators influencing population dynamics. Such goals are typically examined through time-series analyses that describe several aspects of the fluctuation patterns including the amplitude, periodicity, and the estimated ratio of endogenous vs. exogenous influences on population dynamics (Turchin 1999). Prior work has demonstrated substantial support for the occurrence of density dependence in insect populations. Woiwod & Hanski (1992), for example examined data sets containing 263 moth and 94 aphid species, finding strong evidence for first-order density dependence when their analysis was limited to time series >20 years in length. It is clear that long data time series are essential for the detection of density dependence and for understanding variability in population dynamics (Turchin 1995).

The common wasp is native to Eurasia and invasive in several countries including Argentina, Australia and New Zealand (Beggs *et al.* 2011; Archer 2012). These wasps reach the world's highest known densities in the invaded range of New Zealand, of up to 40 nests per ha and 370 wasps per m² of tree trunk (Moller *et al.* 1991; Burne, Haywood & Lester 2015). These high densities have substantial ecological impacts, including high predation rates on invertebrates and the domination of food resources (Toft & Rees 1998; Grangier & Lester 2011). Common wasps have even been observed killing native birds in New Zealand (Moller 1990). Populations of these wasps in Argentina and New Zealand are likely to have arisen from Western Europe and the United Kingdom (Lester *et al.* 2014). The abundance of common wasps within the native range fluctuates substantially (Beirne 1944; Archer 1985, 2001). Worker abundance, nest densities and queen productivity can vary by two orders of magnitude between successive years in England (Archer 1981, 1985, 2001; Archer & Halstead 2014). Much less variation in wasp abundance has been observed in New Zealand (Barlow, Beggs & Barron 2002).

A variety of factors have been hypothesised to contribute to variation in wasp population abundances. Climate has long been cited as a major contributor to inter-annual variation in insect communities (e.g.

Andrewartha & Birch 1954), including in wasp populations (Fig. 1). Common wasps typically overwinter alone as mated queens, with winter conditions representing a bottleneck through which only larger queens with higher fat reserves appear to survive (Harris & Beggs 1995). Colder and wetter conditions in this incipient spring phase of the wasp life cycle have been related to lower wasp abundances (e.g., Akre & Reed 1981; Barlow, Beggs & Barron 2002; Masciocchi, Pereira & Corley 2016). Other researchers, however, have failed to find any relationship between spring weather and variation in annual wasp abundances (Fox-Wilson 1946; Archer 1985). Warmer and drier summer conditions have also been associated with a high abundance of many insects including wasps (Edwards 1980; Archer 1985). Another potential factor influencing annual wasp abundance is intraspecific competition. During spring, high levels of intra and interspecific competition for and usurpation of nest sites can occur (Matthews & Matthews 1979). Competition between workers during the summer period has also been hypothesised to result in the production of poor quality queens after summers of high wasp abundance (Archer 2010). Different authors have argued for and against the role of factors such as climate and competition in regulating wasp populations, without consensus (Table S1, Supporting Information).

Several analyses of wasp population dynamics have previously been developed leading to varying conclusions. Archer (1985) found evidence of a 2-year cycle with years of abundance and scarcity that tend to occur in pairs in the wasps' native range. He also found evidence for a possible 7-year cycle (Archer 1985). Barlow, Beggs & Barron (2002), using a short time series of 13 years in the invaded range of New Zealand found no evidence for 2-year population cycles but did observe significant autocorrelations at lags of 7 and 8 years. They also found some evidence for first-order density dependence. Here, we analysed the population dynamics of the invasive common wasp using an expanded time series containing annual abundance data from its native range in England and the invaded range of New Zealand. Our first goal was to describe the fluctuation patterns, including the detection of any periodicity, and to examine the role of endogenous and exogenous influences. Our second goal was to characterise the structure and estimate the order of density dependence, testing for differences between the native and introduced range. Finally, we developed a novel multivariate dynamic factor analysis model incorporating climatic variables to predict wasp abundances in both countries.

Materials and methods

WASP ABUNDANCE DATA

Long-term data sets were used from four sites in the home range of common wasps (England) and six sites in the invaded range (New Zealand) (Table S2). Data from England were from suction-traps used to sample a range of insects and located in

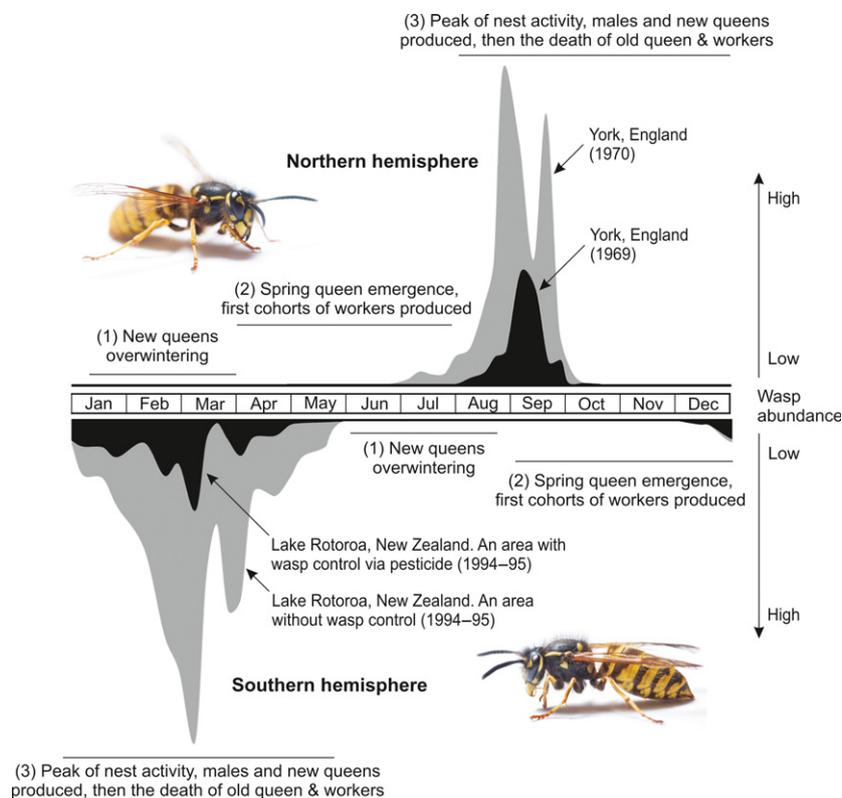


Fig. 1. The annual population dynamics of common wasps (*Vespula vulgaris*) in their native range (York, England; 53.95°N) and the invaded range (Lake Rotoroa, New Zealand; 41.87°S). Data for two sites are shown for each range. In England one year of relatively low abundance is followed by the next year of higher densities. The differences in abundance for the New Zealand data were achieved by pesticide use. For the purpose of our analysis, the timeline is broken into three phases based on previous literature (Table S1). (1) A period when the newly produced queen wasps overwinter in the absence of any workers. Cold and wet conditions in the winter have been hypothesised as a major source of queen mortality, resulting in low worker and nest abundance in the following summer. (2) The queens emerge from their overwintering sites and have been observed to compete to establish new nests. During the early stages of this period they forage for food themselves and produce the first cohorts of workers. High rainfall and cold temperatures have been suggested as major sources of mortality during this 'critical stage' in spring (Akre & Reed 1981). (3) Wasp populations peak in late summer and early autumn. Several hundred new queens per nest are often produced, mate with males, and find overwintering sites. The old nest then collapses and workers die. Population demographic data are from Archer (cited in Edwards 1980), and Toft & Rees (1998). Wasp photographs by Colin McDiarmid. [Colour figure can be viewed at wileyonlinelibrary.com]

Rothamsted (51.809° N, 0.355° W; with dates of 1972–2010) and Silwood (51.398° N, 0.629° W; 1972–1988, and 2000–2010), with a Malaise trap at Leicester (52.633° N, 1.133° W; 1972–2001). These sites were surrounded by a predominantly arable landscape. Suction-traps were 12.2 m tall and were operated without bait or attractant (Macaulay, Tatchell & Taylor 1988). An additional trap at 1.5 m from ground level was operated at Rothamsted. The yearly count of wasps was the total number of worker wasps collected for the period of March until December in each year, corresponding to the northern hemisphere early spring until the beginning of winter. Subsets of all data sets have been analysed previously (e.g., Archer 1985, 2001). Climate data were obtained for each site from a weather station within 20 km of each trap. This weather information was used to calculate estimates of the mean temperature, minimum temperature, and total rainfall for critical periods of the wasp biology and life cycle in the northern hemisphere (Fig. 1, Table S1) that broadly correspond to 'spring' (April to July), 'summer and autumn' (August to December), and 'winter' (January to March). These climate variables and periods were chosen based on previous hypotheses regarding factors that influence wasp abundance (Table S1).

Data from New Zealand were the densities of wasp nests per ha within native *Fuscospora* spp. beech forests of the South Island. Sites were Matakita Valley (42.009° S, 172.520° E), Mt Misery (41.939° S, 172.667° E), Pelorus Bridge (41.301° S, 173.571° E), Rotoiti (41.811° S, 173.850° E), Spooners Range (41.469° S, 172.911° E) and Tiraumea Saddle (41.922° S, 172.621° E). Nests were counted by at least three people slowly walking a 1–2 km strip transect during March or April in each year, from 1988 to 2010. Barlow, Beggs & Barron (2002) describe these study sites and used part of this data set in their analysis of 1988–2000 data. Different measures of wasp abundance were thus used for the New Zealand and English data sets. Wasp nest densities and worker abundance were assessed respectively. For an analysis on population dynamics, however, we consider the different sampling methods provide comparable data for several reasons. Firstly, all sampling methods collected or observed wasps passively (i.e. without bait or attractants). Secondly, wasp nest abundances in England show very similar population dynamics to that of English worker abundance (Archer & Halstead 2014; Archer 2015). The abundance of *V. vulgaris* workers and nest densities are also highly correlated in New Zealand. For example,

Beggs *et al.* (1998) found that almost 90% of the variation in the yearly catch of *V. vulgaris* workers was explained by a linear relationship with variation in nest densities. Finally, one of the four sites in England was sampled using a Malaise trap, though showed very similar population dynamics to the suction-traps. Taken together, these results provide a high degree of confidence that nest and worker abundance are comparable measures for the purpose of our analysis.

To allow intra-site comparisons data from both countries were natural-log transformed to stabilise the variance, after first adding one to the counts at the Rothamsted 1.5 m site due to the presence of a zero value (Table S2). Data from both countries were then standardised (mean-corrected and scaled to have unit variance, e.g. Fig. 2), enabling a meaningful comparison of wasp densities from the native and invaded range. The same climatic variables were used in New Zealand as in the English data analysis, with climate data obtained from Nelson meteorological station (41.271° S, 173.284° E), which is within ~100 km of all six study sites. The spring, summer and winter periods were also the same in New Zealand, except for being offset by 5 months (Fig. 1).

STATISTICAL ANALYSIS

All analyses were conducted in R (R Development Core Team 2016). Our first analysis investigated if wasp populations are regulated by climatic factors in combination with competition in the native and invaded range, and sought to obtain evidence for density dependence acting in a similar fashion in the two regions. We conducted linear regression modelling of the intrinsic rate of increase (r_t), where $r_t = \ln(N_{t+1}/N_t)$, regressed on $\ln(N_t)$ (where

N_t is the wasp abundance in year t) plus relevant weather variables and site effects. The fitted model is thus a Gompertz population model (Gompertz 1825). We assigned dummy variables to each site and site \times wasp abundance combination to test for differences in intercepts and slopes between sites. Climate variables such as average and minimum temperatures covary within and between sites. In England site-specific climate data was available, giving a total of 27 possible climate covariates. Site-specific climate offsets were also calculated and included in the stepwise modelling procedure. To mitigate collinearity issues we averaged across these sites, producing nine climate covariates. We used Akaike's Information Criterion (AIC) as an objective function for stepwise model selection (with both forward and backward search directions) using the *stepAIC* function from the MASS package (Venables & Ripley 2002). In addition, the relative importance of the variables in each regression model was estimated using the *calc.relimp* procedure in the relaimpo package (Grömping 2006). The *calc.relimp* procedure provides estimates of the lmg metric, which gives the sequential R^2 contribution from each variable averaged over orderings among the regressors; lmg values are normalised to sum to 1.

Our second goal in this study was to examine the time series of annual wasp abundances for periodicity or cyclic dynamics, and then develop a model incorporating climatic variables to predict wasp abundances. Estimated autocorrelation functions (ACFs) are commonly used to summarise periodicity or cyclic dynamics. Data standardisation following logarithmic transformation had successfully stabilised the variance (Fig. 2), and we applied site-specific trend corrections to all data (by linear regression on time) to remove any trends prior to calculation of the ACF at each site. We also calculated the partial rate correlation function

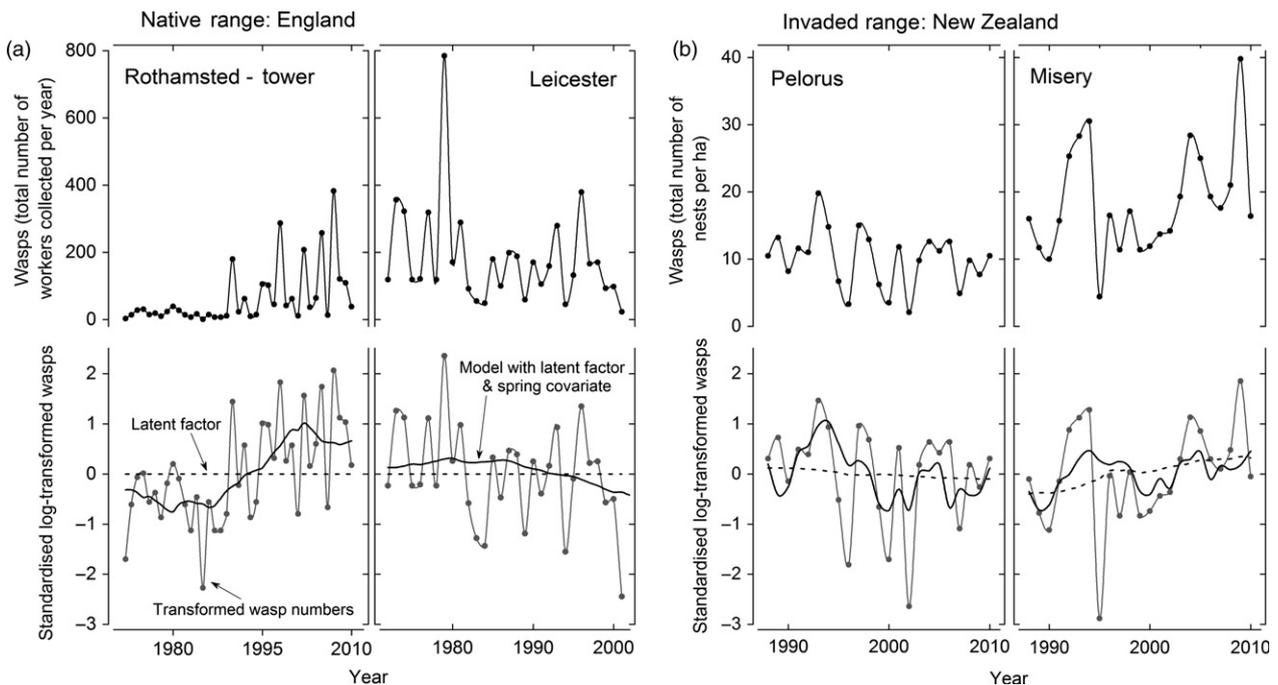


Fig. 2. Examples of wasp population dynamics at four of the ten study sites, before and after natural-log transformation and standardisation from the native range (a), and the invaded range (b). The lower panels also show the estimated latent dynamic trend at each site and the final predicted values, which include the effects of the latent spring weather covariate. Note that wasp population dynamics at Rothamsted changed, being considerably more variable and around a higher level after 1990. This change in dynamics appeared to be associated with a change in local climate conditions at this time (Fig. S1).

(PRCF) for each site (Berryman & Turchin 2001). PRCFs estimate the correlation between r_t and the logarithmic wasp population density at lag i , $\ln(N_{t-i})$, with the effect of intermediate lags 1, 2, ..., $i - 1$ removed, or partialled out. These estimates give insights regarding the order of the negative feedback in the time-series dynamics (Berryman & Turchin 2001). To generate population cycles second-order (or higher) lags are needed. PRCFs are especially appropriate in ecology as they use an appropriate null model for detecting direct or delayed density dependence (Berryman & Turchin 2001). Statistical significance of both ACF and PRCF values was assessed by Bartlett's approximate 95% confidence intervals, $\pm 2/\sqrt{n}$, where n is the number of observations at each site (Berryman & Turchin 2001). We modelled ACF and PRCF values up to a maximum of a 10-year lag, as such long population lags have been suggested for this wasp species (Archer 1985; Barlow, Beggs & Barron 2002) and other insect pests (Myers & Cory 2013).

The two collections of observed wasp abundances and climatic variables in the native and invaded ranges are inherently multivariate in their temporal dependence. A modelling approach that explicitly accounted for this multivariate structure was desirable. Consequently, we used the multivariate autoregressive state-space (MARSS) package (Holmes, Ward & Wills 2012) to provide country-specific maximum likelihood estimates of linear MARSS models fitted to the multivariate wasp time-series data. MARSS models provide an ideal framework for inferring community dynamics, stability, and identifying environmental drivers using long-term time-series data (Hampton *et al.* 2013). Dynamic factor analysis was used to identify underlying common trends for the wasp abundances. Latent (unobserved) common trends represent the dynamic structure of the multivariate data in a smaller number of dimensions than the number of observed time series, using linearly independent combinations of independent random walks. The optimal number of common trends was selected using the small-sample corrected version of Akaike's information criterion (AICc). In addition to estimated factor loadings on the common trends, the observed wasp abundance time series each included a stochastic observation error. The observation errors were modelled with a multivariate covariance structure to allow associations between the series if required. Four common error covariance structures, all available using MARSS, are as follows: errors independent with one common variance; errors independent with all variances different; errors correlated with a single common correlation parameter between each pair of series and with one common variance; and errors correlated with each process having unique correlation parameters and all variances different, i.e. an unconstrained covariance matrix. Selection of the most appropriate error covariance structure was done simultaneously with maximum likelihood parameter estimation, using AICc.

The effects of climatic variables were incorporated in the multivariate models using further latent dynamic factors as covariates. These covariates were estimated, using MARSS and again selected via AICc, to maximise the variance explained in the minimum and average seasonal temperatures and the total rainfall in each season. In a dynamic factor analysis, the latent factors are statistically independent and thus effectively control for any multicollinearity among the potential covariate time series. For further model comparison the AICc weights were also calculated for the selected models. AICc weights sum to unity by construction and are defined for each model as $\exp(-0.5 \times \Delta\text{AICc}) / (\text{sum over all models of } \exp(-0.5 \times \Delta\text{AICc}))$, where ΔAICc gives the change in AICc from the best model.

Results

Wasp densities fluctuated substantially in the native range. For example, at Rothamsted there were several years when only 0, 1 or 2 common wasps were caught during an entire year of sampling. In other years there were as high as 403 wasps caught within a year at this site. The temporal dynamics of annual wasp catch appeared to change around 1990 at Rothamsted (Fig. 2a). After 1990 the wasp population dynamics more resembled those at sites such as Leicester, where there were 5 years in which the annual wasp catch was ≤ 59 and 5 years with ≥ 319 . This increase in wasp abundance at Rothamsted appeared to be associated with an increase in the composite spring weather variable for this area (Fig. S1). The maximum number of workers caught in a year-long sampling period was 1610 at Silwood in 2007.

Wasp densities also fluctuated within the invaded range of New Zealand, though note that the unit of measurement in New Zealand was wasp nest abundance per ha and not worker abundance as in England. For example, at Pelorus Bridge there were 5 years with ≤ 6.2 nests per ha, and 5 years with ≥ 12.9 nests per ha (Fig. 2b). The maximum density of nests observed was 40 nests per ha in Lake Rotoiti in 1998, and the minimum was 1.1 nests per ha, in Matakita Valley in 1996.

DENSITY DEPENDENCE, WITH CLIMATE

We used regression models selected by AIC to test that the intrinsic rate of increase (r_t) for wasp populations is regulated by climatic factors in combination with density dependence, in the native and invaded range. The derived statistical models explained a high proportion of the annual variation in the exponential growth rate of wasp populations, with R^2 values of 0.656 for England (the native range) and 0.593 for New Zealand (the invaded range).

In both countries the most important variable in our regression models was the lag of wasp abundance from the previous year. This result demonstrates a similar and highly significant negative density-dependent relationship in wasp populations from both countries (Table 1, Fig. 3). The estimated coefficient of the lag of $\ln(N_t)$ in the final regression models was remarkably similar in the two countries at -0.893 and -0.859 , for England and New Zealand respectively. These coefficients had associated Img values of 0.597 and 0.564, respectively, showing almost 60% of the variation explained by each model was due to the negative first-order density dependence. The associated 95% confidence intervals of these slopes overlapped, with England 95% CI = $(-1.479, -0.307)$, New Zealand 95% CI = $(-1.026, -0.692)$. Statistically significant within-country variation was observed between sites in these models, indicative of site-specific effects on the exponential growth rate and site-specific interactions with the observed density dependence (Table 1). The relative

Table 1. Results from regression analyses of the exponential growth rate (r_t) of wasp populations. Only those explanatory variables that were chosen by the stepAIC function are shown. lmg values are R^2 values partitioned by averaging over orderings among the regressors; they provide an estimate of the relative importance of each regressor to the model. Variables for each model are ranked according to lmg values, excluding 'Constant' and site variables. The overall R^2 value for the English model was 0.656, and 0.593 for the New Zealand analysis

Country & variable	β (SE)	t	P -value	lmg
England (native range)				
1. Lag of ln(wasps)	-0.893 (0.299)	-2.986	0.003	0.597
2. Spring mean temperature	0.791 (0.143)	5.542	<0.001	0.107
3. Winter rainfall	0.219 (0.048)	4.517	<0.001	0.073
4. Winter mean temperature	0.125 (0.081)	1.543	0.125	0.045
5. Summer mean temperature	-0.314 (0.128)	-2.454	0.016	0.025
Constant	-1.243 (2.370)	-0.524	0.601	
Site(Roth-G*)	-2.142 (1.560)	-1.373	0.172	
Site(Roth-T*)	-1.772 (1.591)	-1.114	0.268	
Site(Silwood)	1.307 (1.671)	0.782	0.436	
Site(Roth-G*) \times Lag of ln(wasps)	0.005 (0.328)	0.015	0.988	
Site(Roth-T*) \times Lag of ln(wasps)	0.0689 (0.330)	0.208	0.835	
Site(Silwood) \times Lag of ln(wasps)	-0.466 (0.339)	-1.376	0.171	
New Zealand (invaded range)				
1. Lag of ln(nests)	-0.859 (0.085)	-10.156	<0.001	0.564
2. Winter rainfall	-0.001 (0.001)	-1.389	0.168	0.106
3. Summer rainfall	-0.001 (0.000)	-3.354	0.001	0.106
4. Spring rainfall	-0.001 (0.000)	-2.603	0.011	0.054
5. Spring minimum temperature	-0.096 (0.045)	-2.131	0.035	0.032
Constant	3.589 (0.373)	9.617	<0.001	
Site(Misery)	0.476 (0.159)	2.997	0.003	
Site(Pelorus)	-0.080 (0.153)	-0.522	0.603	
Site(Rotoiti)	0.470 (0.158)	2.979	0.004	
Site(Spooners)	-0.494 (0.162)	-3.052	0.003	
Site(Tiraumea)	0.352 (0.165)	2.142	0.034	

*Roth-G, Rothamsted 1.5 m site; Roth-T, Rothamsted 12.2 m site.

importance of the climate variables was different for the English and New Zealand sites. In the native range of England, three of the four climatic variables used in the final model were temperature related. Warmer winter and spring temperatures were associated with higher wasp abundances. The only additional variable entered was a positive effect of increasing rainfall in winter (Table 1). For the invaded range of New Zealand, three of the four climate variables used in the model were rainfall related. Increased rainfall in spring, summer or winter was associated with reduced wasp abundances (Table 1). Note that all these fitted coefficients are estimates of the direct (or partial) effect, interpreted as the expected change in the exponential growth rate for a unit change in the particular explanatory variable, under the assumption that all other variables remain unchanged (a *ceteris paribus* interpretation).

WASP POPULATION CYCLES

No evidence was observed for cyclic population dynamics in the native or introduced range of common wasps. ACF estimates for lags 1–5 were not statistically significant in either country. Wasp abundance dynamics at Silwood demonstrated a statistically significant 6-year ACF lag of -0.382. However, we cannot think of a sound biological

explanation for a single site showing a 6-year delayed negative feedback of density on population dynamics. This result is likely to be a spurious correlation. The remaining ACF estimates were typically close to zero, with 94 of the 100 estimated correlation coefficients from both countries having an absolute value less than 0.3 (Fig. 4; Table S3).

Partial rate correlation function showed strong, statistically significant negative first-order dependence at all sites in both countries, with correlation coefficients ranging from -0.662 (Matakitaki Valley, New Zealand) to -0.815 (Silwood, England). This result is consistent with our observation of a significant negative relationship between the intrinsic rate of increase (r_t) and $\ln(N_t)$ when estimated across all sites in each country using the selected regression models (Table 1, Fig. 3). No statistically significant PRCF values were observed for lags 2–6 (Fig. 4; Table S3). A significant 7-year lag of -0.382 was observed at Rothamsted ground site, but at the nearby Rothamsted tower site the corresponding lag was -0.008. Thus we also consider this isolated result to be a spurious correlation.

MULTIVARIATE MODELLING OF WASP DYNAMICS

A single common trend underlying the four English sites was selected as optimal in the native range of common

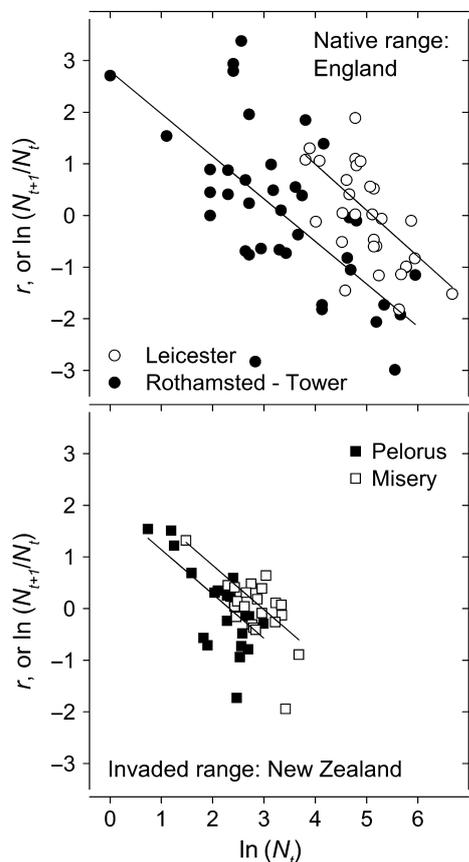


Fig. 3. The observed and predicted exponential rate of increase (r_t , or $\ln(N_{t+1}/N_t)$) of yearly wasp counts in England or autumn wasp nest abundances in New Zealand plotted against $\ln(N_t)$. Predicted values come from the final selected models presented in Table 1.

wasps, using AICc (Table 2). The optimal error covariance structure was with the four error time series correlated, but with a single common correlation parameter between each pair of series and with one common variance. The information available in the 27 English climate variables was incorporated best using a single latent dynamic factor that summarised the nine spring climate variables. Use of any further climate covariates produced fitted models with higher AICc values, suggesting overfitting (Table 2). The AICc weights suggest that the model using the latent dynamic factor summarising spring climate has approximately double the relative importance of the next best model, which did not include any covariates and relied on the estimated common trend to explain movements in annual wasp abundance. However, with the inclusion of the latent dynamic spring factor, no further common trend movement was needed to explain observed wasp abundances. Hence the common trend in the best model for the native range is constant at the value zero for all sites; that is, constant at the mean of the standardised data (Fig. 2a).

In a manner similar to the native range, a single common trend underlying the six New Zealand sites was

selected as optimal in the invaded range of common wasps, using AICc (Table 2). Again the optimal error covariance structure was with the error time series correlated, but with a single common correlation parameter between each pair of series and with one common variance. As in the native range, the information available in all the New Zealand climate variables was incorporated best using a single latent dynamic factor that summarised the three spring climate variables (Table 2). The AICc weights suggest that the model using the latent dynamic factor summarising spring climate is by far the most important of those fitted to the New Zealand data, with a relative model weighting of 97%. In the invaded range, the predominant feature of the observed wasp abundances explained by the latent dynamic factor summarising spring climate was the periods of time above and below the evolving mean level, rather than an overall increase or decrease in level. Hence in the invaded range there is a common trend with estimated non-zero factor loadings, in addition to the modelled effect of the spring climate (Fig. 2b). This inclusion of a common trend in New Zealand, but not in England, may be associated with a lack of spatially close and site-specific climatic data in New Zealand.

Discussion

Invasive species are frequently thought to exhibit different population dynamics in their native and introduced ranges, though there are few comparative long-term analyses for the world's most damaging invasive animals (Parker *et al.* 2013; Frederiksen *et al.* 2014). Our long-term population analysis on social wasps is unusual in this regard. They are considered to be one of the world's worst invasive species, but are less problematic in their native range. Nevertheless, common wasps showed remarkably similar population dynamics in the two countries. Density dependence was the strongest predictor of between-year population dynamics and acted in a similar fashion for both England and New Zealand. Our time-series analysis showed strong first-order or lag-1 effects, but no evidence of higher order or delayed density dependence in either country. Weather in both countries significantly influenced wasp abundance, though in England temperature had the strongest effects while in New Zealand rainfall was more important. 'Successful' predictive modelling in ecology is assumed when statistical models explain >50% of the variation (Turchin 2003). Our models explained 65.6%, and 59.3% of the variation in wasp populations for England and New Zealand respectively.

Our observed result of first-order, negative density dependence in common wasps was not surprising given it has been described as a 'pervasive feature of insect populations' (Woiwod & Hanski 1992). These authors found little or no variation in density dependence within aphid or moth species between localities in England. Our analysis showed a very similar, first-order negative density

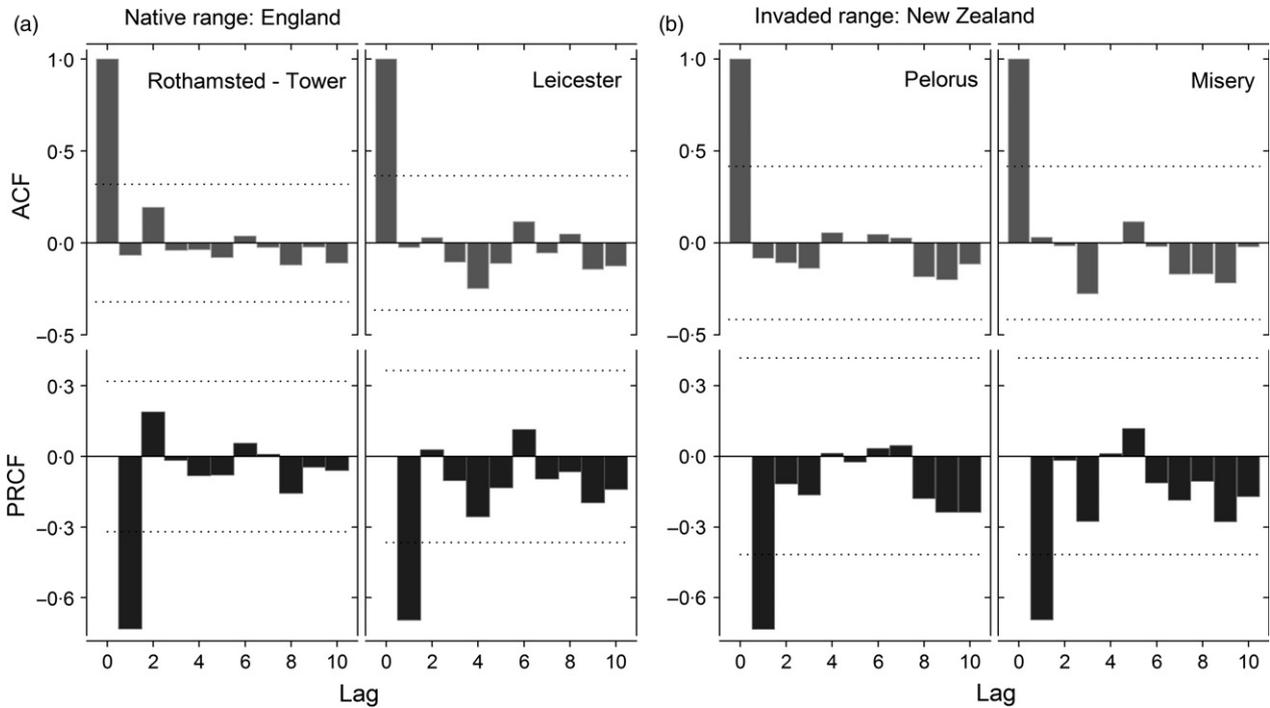


Fig. 4. Autocorrelation functions (ACF) and partial rate correlation functions (PRCF) for wasp populations at two sites from the native range of England (a) and two sites from the invaded range of New Zealand (b). For all sites these correlations were calculated after taking natural logs and then trend-correcting each site by regression on a time trend. The dashed lines represent 5% critical values assuming no correlation, hence correlations outside these limits are significantly different from zero.

Table 2. Country-specific model selection summaries of linear multivariate autoregressive state-space (MARSS) models fitted by maximum likelihood to the wasp multivariate time-series data using the MARSS package

Model rank	Latent climate covariates			L-L	<i>k</i>	AICc	ΔAICc	AICc weight
	Winter	Spring	Summer					
England (native range)								
1		✓		-162.62	10	347.00	0	0.46
2 (no covariates)				-167.80	6	348.25	1.25	0.25
3			✓	-163.59	10	348.94	1.94	0.17
4	✓	✓		-159.79	14	351.06	4.06	0.06
5		✓	✓	-160.40	14	352.26	5.26	0.03
6	✓		✓	-165.60	10	352.96	5.96	0.02
All covariates	✓	✓	✓	-157.91	18	357.67	10.67	0.00
New Zealand (invaded range)								
1		✓		-159.93	14	351.52	0	0.97
2 (no covariates)*				-173.31	7	361.53	10.01	0.01
3		✓	✓	-156.92	20	361.55	10.03	0.01
4*		✓		-166.22	13	361.58	10.06	0.01
5 (no covariates)†				-166.46	13	362.06	10.54	0.00
6	✓	✓		-157.40	20	362.50	10.98	0.00
All covariates	✓	✓	✓	-153.57	26	372.77	21.24	0.00

Seven different models are shown for each country: a model with no latent climate covariates, a model with all three latent covariates, and the five other best-fitting models. They are presented in order of AICc values, with the change in AICc from the best model also shown (ΔAICc), along with the log-likelihood value (L-L) and the number of estimated parameters (*k*). For further model comparison the AICc weights are also given. AICc weights sum to unity and are defined for each model as $\exp(-0.5 \times \Delta AICc) / (\text{sum over all models of } \exp(-0.5 \times \Delta AICc))$. All but one of the selected models included a single common trend underlying the observed multivariate wasp abundances; the exception (marked with †) had two common trends but no covariates. In nearly all models the selected error covariance structure had correlated errors, with a common correlation parameter and a common variance. The two exceptions (marked with *) had uncorrelated errors and a common variance.

dependence for growth rate of wasps on both sides of the world and suggests that similar causal pathways operate in both countries. Previously described mechanisms for negative density dependence include an increasing effect of parasites or pathogens as insect populations increase, or increasing competition for food or resources, which may result in a declining quality of individuals for the next generation.

Barlow, Beggs & Barron (2002) concluded that competition between queens in spring was a likely cause of density dependence in New Zealand. Recent work on insects has provided evidence that a high parental breeding density can lead to a smaller offspring size, decreasing offspring survival, and result in carry-over effects that influence population growth rates in the following generation (Betini *et al.* 2014). Carry-over effects may act in combination with competition to influence wasp abundance. Pathogens and parasites can also have strong density-dependent influences on insect populations (Myers & Cory 2013). Wasps in both countries are afflicted by fungal and viral pathogens (Evison *et al.* 2012; Lester *et al.* 2014, 2015). Prior work has questioned the abundance and role of pathogens or parasites in wasp population dynamics (Potter 1964; Archer 2001). However, Archer (1981) observed that approximately half of 214 common wasp nests examined over a 5-year period in England had irregularities including atypical brood development. Within honey bees such observations are indicative of microbial disease (e.g. Wilson-Rich *et al.* 2009). That nearly half the common wasp nests displayed these irregularities in England (Archer 1981) is perhaps indicative of a substantial influence of microbial disease on wasp populations. Pathogens may even be involved in maternal effects, interact with environmental stressors, and would likely be most prevalent in populations when wasps are highly abundant.

Previous studies have found evidence for higher order or delayed density dependence in common wasp populations. In England, two of the first analyses on wasp time-series data concluded there was a 2- and possibly 7-year cycle in population dynamics (Archer 1985; Turchin & Taylor 1992). The 2-year cycle in England was thought to dissipate after a change in dynamics during the 1980s (Archer 2001; Archer & Halstead 2014). In New Zealand, a previous analysis using a 13-year data set found no 2-year cycles but significant autocorrelation structure for 7 and 8 year periods (Barlow, Beggs & Barron 2002). These 7- or 8-year cycles have always been difficult to explain for wasps, but their absence in our 23-year analysis and the expanded England data sets (e.g. Archer & Halstead 2014) suggests this was a statistical artefact. The only other time-series analysis of a related invasive social wasp species in the southern hemisphere also found evidence for a negative first-order effect but no higher order density dependence (Estay & Lima 2010). Our lack of higher order or delayed density dependence in common wasps is consistent with the finding that delayed density

dependence is not observed more often than expected by chance in insect populations (Woiwod & Hanski 1992). Wasp populations in the UK have long been thought to have highly abundant 'wasp years' and other years when workers and nests are scarce or not observed at all (Beirne 1944; Archer 1985, 2001, 2015; Archer & Halstead 2014). We conclude that these 'wasp years' are not a result of delayed density dependence, but instead are probably a combined effect of low abundance in the previous year in addition to a favourable specific climate in the current wasp season. The remarkably similar dynamics in the native and invaded range of these wasps is encouraging given that density dependence should be a repeatedly measurable characteristic of a species (Woiwod & Hanski 1992). Some variation was observed between sites likely due to environmental differences that include food availability or disease distribution.

The MARSS models highlighted the importance of spring conditions for wasp population dynamics in both the native and invaded range. In each range the spring variable was a composite of temperature and precipitation data. Beirne (1944) found evidence for the effects of spring rainfall on wasp abundance in England. The most recent analyses of wasps in the invaded range have also highlighted the role of spring conditions on wasp abundance in New Zealand (Barlow, Beggs & Barron 2002) and Argentina (Masciocchi, Pereira & Corley 2016). These previous and our current analysis suggest that the incipient stage of the wasp colony formation is the most susceptible to environmental variation. It has long been known that the failure of incipient nests to become established is a major source of mortality in wasp populations. Estimates of incipient colony survival range from 3% to 8% (Brian & Brian 1952; Yoshikawa 1962). Once a colony is established with an adequate number of workers, 'its success is virtually guaranteed' (Spradberry 1973). The high mortality and susceptibility of incipient wasp populations in spring may open a window for wasp management, such as with control programmes that target these early-stage wasp nests.

The regression analysis indicated that the climatic factors significantly associated with wasp abundance differed between countries. Three of the four statistically significant climatic factors for England related to temperature. Three of the four significant factors in New Zealand related to rainfall. There are potential analytical issues such as collinearity between independent variables (e.g. spring temperature and spring rainfall), which have been recognised as influencing results and conclusions in prior time-series analyses (e.g. Masciocchi, Pereira & Corley 2016). The different variables chosen in each country may also be reflective of the differences in environment between countries. England has a much shorter 'wasp season' of around 4 months, compared to c. 6 months in New Zealand (Fig. 1). If the acquisition of heat units in New Zealand is less limiting than in England, it seems reasonable that factors such as rainfall would have more

of an influence on wasp population dynamics in this invaded range. Rainfall has previously been suggested to have a negative effect on wasp populations in southern hemisphere locations (Madden 1981; Barlow, Beggs & Barron 2002; Estay & Lima 2010).

The substantial change in wasp dynamics at Rothamsted in 1990 appeared to further highlight the role of spring conditions on wasp dynamics. There, an increase in the spring weather latent covariate was associated with a dramatically increasing abundance and fluctuation of wasp dynamics (Fig. 2, Fig. S1). Prior to 1990 there was suggestion of a 2-year population cycle (Archer 2001) and relatively low and less variable temporal abundance. An analysis in Poland similarly found a step change in the phenology of the related German wasp (*Vespula germanica*) in the early 1990s. Tryjanowski *et al.* (2010) found queen wasps to be flying and producing workers increasingly early in the years over 1981–2009; they related the changes in population dynamics to increasing temperature and declining rainfall. Similarly, climate change and increasing temperatures have been associated with German wasps being observed to be extending their range northward in Finland (Sorvari 2013). Climate change may have variable effects for different insect species (Bell *et al.* 2015; Ewald *et al.* 2015). Smaller wasp species, such as German and common wasps, have been predicted to be more sensitive to increases in temperature than larger wasps or hornets (Tryjanowski *et al.* 2010). Our results at Rothamsted have broad implications for climate change, where areas subject to a change in spring climate conditions can expect a change in wasp population dynamics. In areas of the invaded range where there is a decline in precipitation we predict an increase in annual wasp abundances.

Common wasps appear to have similar long-term population dynamics in their native and invaded range. The high abundance and pest status of wasps in New Zealand (Beggs *et al.* 2011) appears likely to be driven by a higher food abundance and a longer growing season, perhaps in combination with other factors such as the lack of natural enemies or competitors. Invasive species may not exhibit different population dynamics despite considerable variation in abundances throughout their distribution.

Authors' contributions

P.J.L. and J.H. conceived the ideas and designed methodology; M.E.A., C.R.S., J.H. and P.J.L. prepared the data; J.H. and P.J.L. analysed the data; P.J.L. and J.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Table S2 shows the entire wasp abundance data set.

References

- Akre, R.D. & Reed, H.C. (1981) Population cycles of yellowjackets (Hymenoptera: Vespinae) in the Pacific Northwest. *Environmental Entomology*, **10**, 267–274.
- Andrewartha, H.G. & Birch, L.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, IL, USA.
- Archer, M.E. (1981) Successful and unsuccessful development of colonies of *Vespula vulgaris* (Linn.) (Hymenoptera: Vespidae). *Ecological Entomology*, **6**, 1–10.
- Archer, M.E. (1985) Population dynamics of the social wasps *Vespula vulgaris* and *Vespula germanica* in England. *Journal of Animal Ecology*, **54**, 473–485.
- Archer, M.E. (2001) Changes in abundance of *Vespula germanica* and *V. vulgaris* in England. *Ecological Entomology*, **26**, 1–7.
- Archer, M.E. (2010) The queen colony phase of vespine wasps (Hymenoptera, Vespidae). *Insectes Sociaux*, **57**, 133–145.
- Archer, M.E. (2012) *Vespine Wasps of the World. Behaviour, Ecology & Taxonomy of the Vespinae*, Monograph Aeries Volume 4. Siri Scientific Press, Manchester, UK.
- Archer, M. (2015) Population dynamics of a suburban garden's social wasps (Hymenoptera: Vespidae) over 30 years in Leicester, England. *Entomologist's Monthly Magazine*, **151**, 189–195.
- Archer, M. & Halstead, A. (2014) Population dynamics of social wasps (Hymenoptera: Vespidae) in the Royal Horticultural Society's garden at Wisley, Surrey. *Entomologist's Monthly Magazine*, **150**, 19–26.
- Barlow, N.D., Beggs, J.R. & Barron, M.C. (2002) Dynamics of common wasps in New Zealand beech forests: a model with density dependence and weather. *Journal of Animal Ecology*, **71**, 663–671.
- Beggs, J.R., Toft, R.J., Malham, J.P., Rees, J.S., Tilley, J.A.V., Moller, H. & Alspach, P. (1998) The difficulty of reducing introduced wasp (*Vespula vulgaris*) populations for conservation gains. *New Zealand Journal of Ecology*, **22**, 55–63.
- Beggs, J.R., Brockerhoff, E.G., Corley, J.C., Kenis, M., Masciocchi, M., Muller, F., Rome, Q. & Villemant, C. (2011) Ecological effects and management of invasive alien Vespidae. *BioControl*, **56**, 505–526.
- Beirne, B.P. (1944) The causes of the occasional abundance or scarcity of wasps (*Vespula* spp.) (Hym., Vespidae). *Entomologists Monthly Magazine*, **80**, 121–124.
- Bell, J.R., Alderson, L., Izera, D. *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.
- Berryman, A.A. (1999) *Principles of Population Dynamics and their Application*. Stanley Thornes Ltd, Oxford University Press, Oxford, UK.
- Berryman, A. & Turchin, P. (2001) Identifying the density-dependent structure underlying ecological time series. *Oikos*, **92**, 265–270.
- Betini, G.S., Griswold, C.K., Prodan, L. & Norris, D.R. (2014) Body size, carry-over effects and survival in a seasonal environment: consequences for population dynamics. *Journal of Animal Ecology*, **83**, 1313–1321.
- Brian, M.V. & Brian, A.D. (1952) The wasp *Vespula sylvestris* Scopoli: feeding, foraging and colony development. *Transactions of the Royal Entomological Society of London*, **103**, 1–26.
- Burne, A.R., Haywood, J. & Lester, P.J. (2015) Density-dependent effects of an invasive wasp on the morphology of an endemic New Zealand ant. *Biological Invasions*, **17**, 327–335.
- Edwards, R. (1980) *Social Wasps: Their Biology and Control*. The Rentokil Library, Rentokil Ltd., East Grinstead, UK.
- Estay, S.A. & Lima, M. (2010) Combined effect of ENSO and SAM on the population dynamics of the invasive yellowjacket wasp in central Chile. *Population Ecology*, **52**, 289–294.
- Evison, S.E.F., Roberts, K.E., Laurenson, L., Pietravalle, S., Hui, J., Biesmeijer, J.C., Smith, J.E., Budge, G. & Hughes, W.O.H. (2012) Pervasiveness of parasites in pollinators. *PLoS ONE*, **7**, e30641.
- Ewald, J.A., Wheatley, C.J., Aebischer, N.J., Moreby, S.J., Duffield, S.J., Crick, H.Q.P. & Morecroft, M.B. (2015) Influences of extreme weather,

- climate and pesticide use on invertebrates in cereal fields over 42 years. *Global Change Biology*, **21**, 3931–3950.
- Fox-Wilson, G. (1946) Factors affecting populations of social wasps, *Vespula* species, in England (Hymenoptera). *Proceedings of the Royal Entomological Society of London (A)*, **21**, 17–27.
- Frederiksen, M., Lebreton, J.-D., Pradel, R., Choquet, R. & Gimenez, O. (2014) Identifying links between vital rates and environment: a toolbox for the applied ecologist. *Journal of Applied Ecology*, **51**, 71–81.
- Gompertz, B. (1825) On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London*, **115**, 513–585.
- Grangier, J. & Lester, P.J. (2011) A novel interference behaviour: invasive wasps remove ants from resources and drop them from a height. *Biology Letters*, **7**, 664–667.
- Grömping, U. (2006) Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, **17**, 1–27.
- Hampton, S.E., Holmes, E.E., Scheef, L.P., Scheuerell, M.D., Katz, S.L., Pendleton, D.E. Ward, E.J. (2013) Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, **94**, 2663–2669.
- Harris, R.J. & Beggs, J.R. (1995) Variation in the quality of *Vespula vulgaris* (L.) queens (Hymenoptera: Vespidae) and its significance in wasp population dynamics. *New Zealand Journal of Zoology*, **22**, 131–142.
- Holmes, E.E., Ward, E.J. & Wills, K. (2012) MARSS: multivariate autoregressive state-space models for analyzing time-series data. *R Journal*, **4**, 11–19.
- Lester, P.J., Gruber, M.A.M., Brenton-Rule, E.C., Archer, M., Corley, J.C., Dvorak, L., Masciocchi, M. & Van Oystaeyen, A. (2014) Determining the origin of invasions and demonstrating a lack of enemy release from microsporidian pathogens in common wasps (*Vespula vulgaris*). *Diversity & Distributions*, **8**, 964–974.
- Lester, P.J., Bosch, P.J., Gruber, M.A.M. *et al.* (2015) No evidence of enemy release in pathogen and microbial communities of common wasps (*Vespula vulgaris*) in their native and introduced range. *PLoS ONE*, **10**, e0121358.
- Macaulay, E.D.M., Tatchell, G.M. & Taylor, L.R. (1988) The Rothamsted Insect Survey '12 metre' suction trap. *Bulletin of Entomological Research*, **78**, 121–129.
- MacLeod, C.J., Newson, S.E., Blackwell, G. & Duncan, R.P. (2009) Enhanced niche opportunities: can they explain the success of New Zealand's introduced bird species? *Diversity & Distributions*, **15**, 41–49.
- Madden, J. (1981) Factors influencing the abundance of the European wasp (*Paravespula germanica* F.). *Journal of the Australian Entomological Society*, **20**, 59–65.
- Masciocchi, M., Pereira, A.J. & Corley, J.C. (2016) Local dynamics of worker activity of the invasive *Vespula germanica* and *V. vulgaris* (Hymenoptera: Vespidae) wasps in Argentina. *Ecological Entomology*, **41**, 105–111.
- Matthews, R.W. & Matthews, J.R. (1979) War of the yellow jacket queens. *Natural History*, **88**, 56–67.
- Moller, H. (1990) Wasps kill nestling birds. *Notornis*, **37**, 76–77.
- Moller, H., Tilley, J.A.V., Thomas, B.W. & Gaze, P.D. (1991) Effect of introduced social wasps on the standing crop of honeydew in New Zealand beech forests. *New Zealand Journal of Zoology*, **18**, 171–179.
- Myers, J.H. & Cory, J.S. (2013) Population cycles in forest lepidoptera revisited. *Annual Review of Ecology, Evolution and Systematics*, **44**, 565–592.
- Parker, J.D., Torchin, M.E., Hufbauer, R.A. *et al.* (2013) Do invasive species perform better in their new ranges? *Ecology*, **94**, 985–994.
- Potter, N.B. (1964) A study of the biology of the common wasp, *Vespula vulgaris* L., with special reference to the foraging behaviour. PhD thesis, University of Bristol, Bristol, UK.
- R Development Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at <http://www.R-project.org>.
- Royama, T. (1992) *Analytical Population Dynamics*. Chapman and Hall, London, UK.
- Sorvari, J. (2013) Social wasp (Hymenoptera: Vespidae) beer trapping in Finland 2008–2012: a German surprise. *Entomologica Fennica*, **24**, 156–164.
- Spradbery, J.P. (1973) *Wasps. An Account of the Biology and Natural History of Social and Solitary Wasps*. University of Washington Press, Seattle, Washington DC, USA.
- Toft, R.J. & Rees, J.S. (1998) Reducing predation of orb-web spiders by controlling common wasps (*Vespula vulgaris*) in a New Zealand beech forest. *Ecological Entomology*, **23**, 90–95.
- Tryjanowski, P., Pawlikowski, T., Pawlikowski, K., Banaszak-Cibicka, W. & Sparks, T.H. (2010) Does climate influence phenological trends in social wasps (Hymenoptera: Vespinae) in Poland? *European Journal of Entomology*, **107**, 203–208.
- Turchin, P. (1995) Population regulation: old arguments and a new synthesis. *Population Dynamics: New Approaches and Synthesis* (eds N. Cappuccino & P. Price), pp. 19–40. Academic Press, New York, NY, USA.
- Turchin, P. (1999) Population regulation: a synthetic view. *Oikos*, **84**, 153–159.
- Turchin, P. (2003) *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, NJ, USA.
- Turchin, P. & Taylor, A. (1992) Complex dynamics in ecological time series. *Ecology*, **73**, 289–305.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York, NY, USA.
- Wilson-Rich, N., Spivak, M., Fefferman, N.H. & Starks, P.T. (2009) Genetic, individual, and group facilitation of disease resistance in insect societies. *Annual Review of Entomology*, **54**, 405–423.
- Woiwod, I.P. & Hanski, I. (1992) Patterns of density dependence in moths and aphids. *Journal of Animal Ecology*, **61**, 619–629.
- Yoshikawa, K. (1962) Introductory studies in the life economy of polistine wasps. I. Scope of problems and consideration on the solitary stage. *Bulletin of the Osaka Museum of Natural History*, **15**, 3–27.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Wasp abundances and spring weather at Rothamsted, England.

Table S1. Factors previously associated with variable wasp population dynamics.

Table S2. Wasp abundances in England from suction-traps, and in New Zealand from nest densities per ha.

Table S3. Estimated autocorrelation functions (ACF) and partial rate correlation functions (PRCF) of wasp abundances.