CHAPTER 4

Spatially explicit host-parasitoid relationships: density dependence revisited

INTRODUCTION

The realisation of the importance of space in species interactions and their responses to resources has increased significantly over the last decade (Ives & Klopfer 1997; Godfray *et al*. 2000; Stewart *et al*. 2000; Liebhold & Gurevitch 2002; McGeoch & Price 2004). Spatial variation in the densities of individuals of one species may result in higher order aggregation in others (e.g. interactions between herbivores and their host plants, or predators and their prey) (Logerwell *et al*. 1998; Bohan *et al*. 2000; Wiens 2000; Winder *et al*. 2001; Brewer & Gaston 2002). One well known example is the marked effects spatial variation in a species' abundance can have on the mortality levels imposed by its natural enemies (Hassell & May 1974; Godfray *et al*. 2000; Hassell 2000), i.e. when host (prey) individuals are aggregated, natural enemies may concentrate their search in high density areas (Hassell & May 1974; Dolman & Sutherland 1997; Godfray *et al*. 2000). For example, randomly searching parasitoids are thought to have lower attack rates when hosts are aggregated because search time is wasted by foraging in empty patches (Murdoch & Stewart-Oaten 1989; Hassell and Pacala 1990). By contrast, a non-random search relative to host density will result in increased attack rates when hosts are aggregated (Hassell and Pacala 1990, Kareiva 1990). Inverse and direct patterns of density dependent parasitism therefore result under these conditions.

Despite obvious selective advantages to natural enemies in targeting high abundance patches (i.e. reduced search time within patches and travel time between patches) (Charnov 1976, Cook & Hubbard 1977), patterns of natural enemy-induced mortality of insect herbivores have frequently been found to be density independent (Hassell & May 1974; Lessells 1985; Stilling 1987; Walde & Murdoch 1988; Norowi *et al*. 2001). Few natural

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enemy-host interactions have been more extensively examined than herbivore insect-parasitoid interactions. Review of the frequency of detecting density dependence in parasitism rates demonstrates that approximately half of these relationships were density independent, while the remainder equally divided between direct and inverse density dependence (Lessells 1985; Stilling 1987; Walde & Murdoch 1988). The low frequency of density dependence is not necessarily unexpected, as the factors influencing interactions between herbivores and their parasitoids are numerous (Hassell & May 1974; Lessells 1985; Godfray *et al*. 2000). For example, the absence of density dependent parasitism has been considered to be a consequence of a wide array of factors, including the absence of an aggregative response by the parasitoid (Loch & Zalucki 1998), interference between parasitoids (Sutherland 1983; Visser *et al*. 1999), sequential parasitism (Lessells 1985), mortality inflicted by hyperparasitoids (Loch & Zalucki 1998) or other natural enemies of parasitoids (Strong 1989), host spatial distribution (Iwasa *et al*. 1981; Lessells 1985; Driessen *et al*. 1995), low and variable host abundance (Hails & Crawley 1992), egg-laying potential (Hassell 1982; Lessells 1985), and finally, parasitoid searching capacity (Loch & Zalucki 1998).

Studies conducted at inappropriate scales for the search behaviour of the natural enemy concerned, have also been shown to be responsible for the failure to detect density dependence (Heads & Lawton 1983; Ray & Hastings 1996). Density dependence may not be detected if studies are conducted at the 'wrong' spatial scale (extent of the study arena) (Ray & Hastings 1996). The scale at which parasitism rates are investigated has also been shown to influence the type of density dependence detected (Heads & Lawton 1983; Hails & Crawley 1992; Norowi *et al*. 2000; but see, Walde & Murdoch 1988; Freeman & Smith 1990; Rothman & Darling 1990; Stiling *et al*. 1991). Generally, when scale increases from the 'plant part' to 'whole plant' to 'several plant' scales, density dependent parasitism changes from inverse to direct density dependence to density independence (Norowi *et al*. 2000). However, although the range of densities increases with increasing scale, the number of replicates in studies tends to decline, making it difficult to distinguish statistical artefact from ecological reality when investigating the detection of density dependence (Hails & Crawley 1992). Nonetheless, for appropriately scaled studies ("scale at which natural enemies recognize and respond to changes in host density" *sens*u Hails & Crawley 1992) density dependence should be detected if present (Ray & Hastings 1996) and reflect a biologically realistic response (Heads & Lawton 1983).

Finally, the failure to detect spatial density dependence has also been attributed to the low statistical power (Type II errors) of tests used (Hails & Crawley 1992; Dolman & Sutherland 1997). For example, binomial regression, one method of detecting density dependence in parasitism rates, has acceptable Type I error levels, but runs a greater risk of making a Type II error, especially when underlying density dependence is weak (Hails & Crawley 1992). Furthermore, recent advances in the analysis of spatial data and in describing spatial heterogeneity (Legendre *et al*. 2002; Perry *et al*. 2002) highlight some issues that suggest that the quantification of host-parasitoid relationships (HPR's) warrant reconsideration. First, the spatial non-independence of host density counts (i.e. the sample points) (and the resulting increase in Type I error rates; see Legendre & Legendre 1998) in HPR's dictate that the spatial position of counts must be considered in such analyses. Second, because density dependence is specifically a proportional response of a parasitoid species to the spatial pattern of aggregation of its host (Hassell & May 1974), a biologically relevant, spatial measure of aggregation is most appropriate (see Perry 1998). Therefore, there is clearly a need to explicitly consider the spatial position of hosts (i.e. spatial references of sampling point) when examining HPR's, and the inclusion of spatial information in such analyses (i.e. spatially explicit analyses) may provide further insight into density dependent relationships.

Host-parasitoid relationships

Several types of HPR's have been used to quantify patterns of density dependent parasitism (Table 1). The behavioural and population functional responses investigate individual and population attack rates in relation to host density, whereas the aggregative response quantifies the tendency for parasitoids to aggregate in areas of high host density (Table 1). The proportion of parasitised hosts (rather than number) per patch can also be used, providing an indirect description of parasitoid response to host density (Hassell 1982). In the HPR literature, the term ‘spatial density dependence’ has become synonymous with the latter relationship, i.e. between the proportion of parasitised hosts and host density across patches (Lessells 1985; Stilling 1987; Walde & Murdoch 1988; Pacala & Hassell 1991) (Table 1). This arose from the more commonly investigated relationship between host density and overall site parasitism over time, i.e. temporal density dependence (Holyoak 1994; Hunter & Price 1998)

Table 1. Different types of host-parasitoid relationships (HPR's) used to quantify patterns of parasitism as a function of host density, divided into spatially explicit and non-explicit relationship categories. The applications of these relationships are also indicated. Numbers in superscript denote source of terminology or example of recent use. DD, density dependence; DI, density independence.

Types of HPR's Different forms of a HPR	Host-parasitoid interaction	Synonyms	Application
	Spatially non-explicit relationships		
Behavioural functional response [1]	Relationship between the attack rate of an individual parasitoid and host density on one or a few plants [1, 2, 3]	-	Behavioural studies [1]; Optimal foraging models [4]
Population functional response [1]	Relationship between average parasitoid attack rate and mean host density among plants in a study arena [1]	-	Modelling host-parasitoid dynamics [1]; Studies on population dynamics [1]
Type I curve [5]	Parasitoid attack rate increases linearly with increasing host density but ceases to increase after some threshold density	-	Density independence (at high host densities)
Type II curve [5]	Parasitoid attack rate decelerates with increasing host density	-	Inverse DD
Type III curve [5]	Parasitoid attack rate accelerates with increasing host density but decelerates after some threshold density	-	Direct DD (at low host densities)

Table 1. continued

Types of HPR's Different forms of a HPR	Host-parasitoid interaction	Synonyms	Application
Aggregative response [6]	Relationship between numbers of foraging parasitoids the density of the host per patch [2, 6]	Spatial distribution of foraging parasitoids [6]	Modelling of parasitoid foraging behaviour [2]
Spatial density dependence [5, 7, 8, 9]	Relationship between proportion of parasitised hosts per patch and host density, across patches [6] (Positive correlation between parasitism rate and host density across patches [5])	Pattern of parasitism [6]; Aggregative response* [7]; Spatial aggregation of deaths [9]; Type of parasitoid aggregation [10]	Traditional method of detecting DD [5, 7, 8, 9]
Direct density dependence [6]	Proportion parasitised per patch increases with increasing host density [6]	Density dependent aggregation [10, 11]	
Inverse density dependence [6]	Proportion parasitised per patch decreases with increasing host density [6]	Inverse density-dependent aggregation [10, 11]	
Density independence [6]	Proportion parasitised per patch is unaffected by host density [6]	Density-independent aggregation [10, 11, 12]	

Table 1. continued

Types of HPR's Different forms of a HPR	Host-parasitoid interaction	Synonyms	Application
	Spatially explicit relationship		
Spatially associated density dependence	Degree of spatial association between parasitism rate and host abundance	Spatially explicit matching	Proposed new method of detecting DD
Significant association	Matching in spatial pattern of proportion parasitised and host density greater than expected by chance	-	Indicates direct DD
Significant dissociation	Spatial mismatching between proportion parasitised and host density greater than expected by chance	-	Indicates inverse DD
Non-significant association or dissociation	Matching or mismatching between proportion parasitised and host density is no different from expected by chance	-	Indicates density independence

[1] Ives *et al*. 1999; [2] Sutherland 1983; [3] Montoya *et al*. 2000; [4] Iwasa *et al*. 1981; [5] Walde & Murdoch 1988; [6] Hassell 1982; [7] Heads & Lawton 1983; [8] Hassell *et al*. 1987; [9] Hails & Crawley 1992; [10] Klopfer & Ives 1997; [11] Gross & Ives 1999; [12] Pacala & Hassell 1991; * denotes authors use term interchangeably.

Although the population functional response (based on the individual functional response of each parasitoid in the population) (Table 1) has resulted in valuable insights on how variability in individual parasitoid behaviour and spatial pattern of host abundance influence resulting patterns of parasitism (Hassell 1982; Gross & Ives 1999; Ives *et al.* 1999), such investigations are logistically difficult and may be hampered by scale limitations (Ives *et al.* 1999). In addition, despite the aggregative response being important for understanding non-random parasitoid search behaviour, the number of foraging parasitoids does not impact on host population dynamics directly (Hassell 1982; Sutherland 1983; Lessells 1985). By contrast, spatial density dependence depends on the aggregative response (Hassell 1982, Heads & Lawton 1983), behavioural and population functional responses (Hassell 1982; Gross & Ives 1999), parasitoid interference (Sutherland 1983), patch residence time and travel time between patches (Hassell & May 1974; Driessen *et al*. 1995), as well as the foraging strategy employed (Waage 1979; Iwasa *et al*. 1981; Driessen & Bernstein 1999). Therefore, because the proportion of parasitised hosts provides a summary of all factors that may influence mortality as a function of host density, and because it is readily measured, it is most often used when examining HPR's for density dependent parasitism (Hassell 1982; Pacala & Hassell 1991, Hassell 2000).

Spatial density dependence is considered to reflect between-patch variation in the risk of parasitism between individuals in a host population, i.e. 'host density dependent heterogeneity' (patch parasitism risk dependent on host density) *sensu* Hassell (2000). This depends on the frequency distribution of the number of hosts and parasitoids per patch (Hassell 2000). For example, models of direct spatially density dependent parasitism assume that parasitoids will aggregate where hosts are aggregated, the number of hosts per patch being described by the negative binomial distribution (Pacala & Hassell 1991; Hassell 2000). Importantly, however, the spatial positions of these patches relative to each other are not considered. This measure of aggregation (spatial heterogeneity *sensu* Wiens 2000), represented by the frequency distribution of counts, is a spatially non-explicit measure of the degree of aggregation (Perry & Hewitt 1991; Perry 1998). The effect of explicitly considering the spatial positions of these count data on the relationship between the proportion of parasitised hosts per patch and host density across patches (spatial density dependence) has not previously been investigated.

Spatially explicit aggregation in host abundance

Lloyd (1967) first proposed that the detection of density dependence was a function of the importance of host crowding (which is a measure of aggregation). Traditionally, aggregation in host abundance has only been defined by the frequency distribution of number of hosts per patch (e.g. May 1978; Pacala & Hassell 1991). However, the spatial explicitness of the measure used to quantify spatial pattern has been shown to affect if aggregation is present (Chapter 4). For example a spatially non-explicit measure such as an overdispersed frequency distribution indicates only that the count size associated with sample points are aggregated, but not physically where in the study arena this aggregation occurs (Perry *et al*. 1999). The spatial position of aggregation is, however, biologically highly relevant in the detection of density dependence. For example, a patch with low host abundance may be more heavily parasitised if it occurs close to a neighbouring patch with high host abundance that attracts parasitoids to the area. Failure to consider spatial position may in such instances weaken the quantified relationship, and the likelihood that significant spatial density dependence is detected.

Spatial Analysis by Distance Indices is a measure that identifies spatially explicit aggregation (Chapter 4). This measure has greater power to detect departures from random spatial pattern by using all available spatial information (Perry 1998). Although not applied in this context previously, this method also permits the biologically relevant matching of the physical position of aggregation in host density with that of parasitism rate, i.e. spatially associated density dependence (Table 1). Spatial association is a method that is able to determine overall and local (spatially explicit) matching in spatial pattern such as this (Perry & Dixon 2002). By determining the strength of spatial association a test for density dependence is made spatially explicit (Table 1). Furthermore, because spatial association compares the degree of spatial pattern at a shared position of the counts of two variables, instead of only the counts themselves, this method has been empirically shown to have greater power to detect significant relationships between spatially referenced variables (Winder *et al*. 2001). To date no other method has considered the aggregation of hosts (i.e. host density) other than non-explicitly. Even the improvement made by Roland and Taylor (1997) on the binomial regression method, by allowing for spatial non-independence in parasitism rate, does not account for spatial non-independence in, or physical position of host density.

The question that remains unanswered in HPR's, is therefore, does data on the physical spatial position of hosts, in addition to their abundance, affect the type of density dependence observed at a given scale? Using field data on insect-host abundance and parasitism rate, this study tests if a spatially explicit description of host aggregation differs from the traditional, spatially non-explicit methods of detecting dependent parasitism. This is done by comparing spatially non-explicit (spatial density dependence) and explicit (spatially associated density dependence) methods of detecting density dependence, in the type (i.e. direct, indirect or density independence) of density dependence quantified. To my knowledge this will be the first empirical test of spatially explicit density dependence in a HPR. Therefore, this study will indicate whether or not considering host abundance at a sampling point relative to neighbouring points is important for the detection of density dependence.

METHODS

Study Area

Gonometa postica populations were examined at five localities within the known (historic and recent records) outbreak range of this species, spanning a distance of 400km between the two furthest localities. The localities were Vryburg (26°59'S, 24°40'E) and Hotazel (27°15'S, 23°03'E) in North-central South Africa and Gabane (24°37'S, 25°46'E), Kumukwane (24°38'S, 25°40'E), and Kopong (24°31'S, 25°48'E) in South-Eastern Botswana. The dominant woody host species utilized by *G. postica* at the first two localities was *Acacia erioloba* Meyer and at the remainder, *Acacia tortillis* Hayne (both Mimosaceae) (Veldtman *et al*. 2002).

One site was selected at each locality, with two at Vryburg (~ 1.5 km apart). Sampling was standardized by delimiting an approximately rectangular area incorporating 100 trees at each site to compensate for possible tree-density differences between host-plants and localities. An initial minimum of 40 first-generation cocoons per site was a prerequisite for site selection.

G. postica is bivoltine and overwinters in pupal diapause. When diapause is broken in early spring (September to October), emerging moths mate and lay eggs to form the first generation, which start pupating after two months (November to December). A varying

proportion of these pupae undergo rapid development and emerge to give rise to the second generation in mid summer (December to January), which pupate in early autumn (March to April). The un-emerged first generation pupae and second generation pupae enter diapause, emerging only the following spring. Generations are readily distinguishable based on cocoon appearance. New cocoons are covered in a dense layer of setae and their colour contrasts sharply with older, more faded cocoons. Although cocoons can persist on trees for far longer, cocoons older than the previous generation cannot be accurately assigned to a specific generation and were not considered.

Surveys of sites commenced in winter (June to July, 2000) and were repeated in mid summer (January, 2001). During the first survey, the number and fate of overwintering pupae were recorded. With the second survey the resulting fate of those individuals that were alive in the first survey as well as the number of new first generation pupae were recorded. Similarly, the fate of these first generation pupae was followed (two subsequent surveys repeated at same periods as above) till mid summer of the following year (January 2002).

Cocoon sampling

Within each site every tree was carefully searched for cocoons. Cocoons were inspected to determine if the pupa inside the cocoon was i) parasitised, ii) alive, iii) dead as a result of unknown causes or iv) had successfully emerged. This was indicated respectively by the i) presence or ii) absence of small emergence hole(s), iii) light weight of the cocoon or iv) a single large anterior emergence hole. Parasitoid species responsible for parasitism may be identified from the shape and size of emergence holes left in the cocoon wall of a parasitised pupa (Veldtman *et. al* 2004.). Consequently, the number of pupae and number of pupae parasitised by each parasitoid species, per tree were counted.

The position of each tree within a site was measured at the main trunk of the tree with a hand held Global Positioning System (GPS). For trees in close proximity to each other the direction and distance between the two trees were noted and assigned to one of three categories (half, quarter and a tenth of the third (last) decimal of a minute) based on hand drawn maps which specifically documented this fine scale distribution of trees. These spatial co-ordinates were used in all spatial analyses.

For the investigation of density dependence, only sampling points (trees) with at least one pupa were included in analyses, as parasitism events can logically not be observed if there are no pupae. At each site, pupae parasitised by different species of parasitoid were either analysed individually, or collectively ('all species') as a measure of total parasitoid mortality (see also Heads & Lawton 1983; Williams *et al*. 2001).

Although all the parasitoids species considered here parasitise the final instar larvae of *G. postica*, we assume that pupal abundance is a good approximation of final instar abundance. This assumption is based on support from field observations that final instar larvae have a low probability of leaving their final food plant to pupate. Final instars were seldom observed moving between plants, approximately 90% of all pupae are found on the larval host plant, and large quantities of larval frass have been observed under trees with high numbers of pupae. However, if this assumption were incorrect we would not expect any direct density dependent relationships regarding parasitism rate. Using the pupal stage also has advantages. Because parasitised larvae cannot be identified in the field, larvae would have to be collected in order to determine the exact relationship between host abundance and parasitism rate. However, premature removal may prevent an unknown number of parasitism events. A study of density dependent pupal parasitism should thus be seen as a practical surrogate for determining the impact of larval parasitoids on this host species. However, at within tree-level analyses this assumption may easily be violated.

Quantification of host parasitoid relationships

Five methods of detecting density dependence were used in this study to allow the quantified relationships of spatially non-explicit and spatially explicit methods to be compared (Table 2). In the following sections these methods and their previous use in the test of density dependence are described.

Spatial density dependence

The relationship between parasitism rate and host density has most commonly been quantified using simple linear regression after arcsine square-root transformation of the proportion of hosts parasitised (Zar 1984; Williams *et al*. 2001, and Lill *et al*. 2002). However,

Table 2. Methods for quantifying traditional spatial density dependence and spatially associated density dependence. LS, Least squares; ML, Maximum likelihood; SADIE, Spatial Analysis by Distance IndicEs; expo, exponential; log, logarithmic; a and b are constants.

Method	Estimation method	Dependent variable		Independent variable/s		Examples of use
		Y	Form	X	Form	
Spatial density dependence						
1. Arcsine square-root	LS	Proportion of parasitised hosts	$\sin^{-1}\sqrt{y}$	Number of host individuals	untransformed	1, 2, 3
2. Regression function comparison	ML	Number of parasitised hosts	*linear*: y *expo*: y *log*: $\log_e y$ *power*: $\log_e y$	Number of host individuals	*linear*: a + bx *expo*: $\exp^x$ *log*: log a + bx *power*: x^b	4, 5
3. Binomial regression	ML	Proportion of parasitised hosts	log(y/(1 - y)	Number of host individuals	untransformed	6, 7, 8
4. Binomial regression with spatial terms	ML	Proportion of parasitised hosts	log(y/(1 - y)	i. Number of host individuals; ii. Patch location	i. untrans-formed ii. significant 3rd order polynomial terms of locality co-ordinates	9
Spatially associated density dependence						
5. Spatial association	SADIE	Rounded integer of proportion	proportion multiplied by 10	Number of hosts	untransformed	this study

[1] Zar 1984; [2] Williams *et al*. 2000; [3] Lill *et al*. 2002; [4] McCullagh & Nelder 1989; [5] Srivastava & Lawton 1998; [6] Trexler *et al*. 1988; [7] Hails & Crawley 1992; [8] Crawley 1993; [9] Roland & Taylor 1997.

this transformation may not be adequate to meet least squares assumptions for proportion parasitised data (Crawley 1993).

Alternatively, a relationship between two variables can be identified as accelerating, decelerating or constant by fitting different regression functions (Savage 1996) and determining the model with the best fit (Srivastava & Lawton 1998). Because several models may fit such a relationship (May 1975), a model that fits significantly better than alternatives (after penalisation for multiple terms; McGill 2003) has to be identified. Linear, exponential, logarithmic and power functions were fitted to each data set using generalized linear modeling (assuming a Poisson or negative binomial distribution as appropriate) by using different combinations of the untransformed and transformed dependent (link functions either identity or natural logarithm) and independent variables (untransformed or natural logarithm) (McCullagh & Nelder 1989; Srivastava & Lawton 1998). The best fitting model was identified by comparing the log likelihood ratio statistic (difference in log-likelihood score of two competing models against the expectation of the chi-squared distribution; see Dobson 2002, p76) of competing models. All regressions were done using the SAS (PROC GENMOD) (SAS Institute Inc., Cary, New York).

Generalised linear models assuming a binomial error distribution provide a statistically superior option for the regression of percentage parasitism data (Hails & Crawley 1992; Crawley 1993), even when percent parasitism can be successfully transformed to meet the assumption of normality (Quinn & Keough 2002) and after stabilising the variance (Collett 1991). When the numbers of successes, for example parasitism events, are bounded between 0 and the number of hosts available in a patch, a binomial probability model should be used (Trexler *et al*. 1988). A generalized linear model assuming a binomial error distribution was used to determine the relationship between parasitism rate and host density (Trexler *et al*. 1988; Hails & Crawley 1992; Crawley 1993).

This method was also modified to take spatial non-independencies of samples into account by adding spatial terms identified by trend surface analysis (Roland & Taylor 1997). Spatial terms that significantly contributed to explaining variation in parasitism rate (significant terms from the 3rd order polynomial of latitude and longitude records of each tree) were first added in the model. Hereafter host density was added to the model and the estimate of this variable was determined.

Spatially associated density dependence

Just as a linear regression between number of parasitised hosts and available hosts cannot be negative, significant positive spatial association between these two counts will be an artefact of the analysis because number of pupae parasitised is a proportion of the number of pupae (see Brett 2004). To adjust for this, proportions were transformed to integers after multiplying with a constant and rounding to the nearest integer, such that the standard SADIE method can be used with proportional data (Perry *et al*. 1999). The proportion of parasitised pupae (from here on parasitism rate) was subsequently multiplied by 10, a constant that rendered the proportion comparable to the number of hosts (usual maximum range was 20 pupae). We propose that density dependent parasitism can be inferred when the proportion of parasitised pupae is spatially associated with the number of hosts. We refer to this relationship as spatially associated density dependence (Table 1).

Significance of associations was determined by comparing X to critical values for the randomised distribution of overall association, using the 97.5^{th} and 2.5^{th} centiles for a desired 95% confidence interval (Perry & Dixon 2002), and the maximum critical value (derived from the number of simulations (153 times) multiplied by the number of sample points in the data) to determine significance at $p < 0.001$. SADIE clustering and association statistics may be affected by the number and spatial position of patches in data sets (Xu & Madden 2003). However, the implications for multi-patch patterns, as found in this study, are limited (Xu & Madden 2003), and the issues these authors raise therefore do not affect the results we report. The degree of matching between two sets of count data sharing a set of spatial references was determined with spatial association statistics using SADIEShell v. 1.21 software (http://www.rothamsted.bbsrc.ac.uk/ pie/sadie/SADIE_downloads_software_page) (Winder *et al.* 2001, Perry & Dixon 2002).

RESULTS

Only four parasitoid species resulted in more than 5% parasitism in *Gonometa postica* (Table 3). Sites with high pupal abundance did not have higher parasitism rates than low abundance sites (Table 3). On average (± SE) there were 319 (± 66) pupae per site occupying

Table 3. Number of *Gonometa postica* pupae and the percentage parasitised at surveyed sites. The number of pupae, number of parasitised pupae as well as percentage parasitised (individual species or all combined) per site is given for parasitoid species responsible for more than 5% parasitism. The number of trees with at least one pupa or one parasitised pupa (out of 100 trees), as well as the percent of host occupied trees with at least one parasitised pupae is also given.

Locality	Gene-ration	Number of		Parasitoid species or category	Number of parasitised		Overall % parasitised	
		pupae	trees		pupae	trees	pupae	trees
Vryburg1	1	202	53	?*Palexorista* sp.	117	40	57.9	75.5
				All species	150	46	74.3	86.8
Vryburg2	1	426	55	*Brachymeria* sp.	69	23	16.2	41.8
				P. semitestacea	83	34	19.5	61.8
				All species	192	42	45.1	76.4
Gabane	1	505	60	*Brachymeria* sp.	36	17	7.1	28.3
				P. semitestacea	37	18	7.3	30.0
				All species	100	35	19.8	58.3
	2	439	56	*Brachymeria* sp.	64	25	14.6	44.6
				P. semitestacea	31	15	7.1	26.8
				All species	128	32	29.2	57.1
Kumukwane	1	252	51	?Tachinidae sp.	27	18	10.7	35.3
				P. semitestacea	23	17	9.1	33.3
				All species	75	34	29.8	66.7
Kopong	1	92	38	*P. semitestacea*	10	9	10.9	23.7
				All species	20	16	21.7	42.1

52 (± 3) trees. Single parasitoid species parasitised an average of 50 (± 10) pupae on 22 (± 3) trees, while all parasitoids together parasitised 111 (± 25) pupae on 34 (± 4) trees per site. The number of pupae was usually unequally distributed over the site with few trees with high abundance and many with few pupae, resulting in marked differences in host abundance at the between plant scale.

Quantification of host density-parasitism relationships

Spatial density dependence

Using the arcsine square root method, five significant relationships between parasitism rate and host density were found (Table 4). All five had positive slopes (although small) and therefore indicated direct density dependence (e.g. Fig. 1). With regression function comparison, linear and power models generally provided a significantly better fit to the relationship between number of pupae and parasitised pupae than exponential or logarithmic models (Table 4). Therefore, relationships were identified as exclusively density independent (linear or exponent of power model equal to zero) by this method, when it was possible to discriminate statistically between the four alternative models (e.g. Fig. 2). The fit of binomial regression models to parasitism rate, without (standard) or with the inclusion of spatial terms, was adequate (deviance per degree of freedom close to unity, McCullagh & Nelder 1989) in most cases (Table 4). Using standard binomial regression, three significant relationships were identified, all of which were inversely density dependent and weak, with pupal density explaining only between 7-11 % of the deviance in parasitism rate (e.g. Fig. 3). Binomial regression with spatial terms, however, only indicated one significant inversely density dependent relationship with the other two relationships identified by standard binomial regression becoming non-significant.

Table 4. Relationship between parasitism rate and pupal density quantified with alternative methods. Method 2 results with different letters in superscript denote significant differences and rank with respect to best fitting curve (a > b > c). Method 3 results show percentage deviance explained followed by the sign of the relationship in brackets. Method 4 results show the percentage deviance explained by host density after removing significant locational (spatial) terms. Method 5 results show significant overall association (*X*) (ranging between 1 (perfect association) and –1 (perfect disassociation)) and maximum simulated association value from randomisation procedure. Values in bold denote significant density dependence; *, ** and *** are $p < 0.05$, 0.01 and 0.001.

Site (sample size)	Methods										
	1. Arcsine square-root		2. Regression function comparison				3. Binomial regression	4. Binomial regression with spatial terms		5. Spatial association	
	F statistic	slope	% Deviance explained (DE)				% DE	Spatial terms	% DE by host density	*X*	Max. simul. value
			Linear	Exp	Log	Power					
Vryburg1 (n = 53)											
?*Palexorista* sp.	0.14	0.008	73.4 [a]	62.5 [b]	60.0 [c]	73.7 [a]	2.45	x^2	0.71	**0.310***	0.393
All species	0.00	0.000	82.8 [a]	71.9 [b]	67.4 [c]	82.9 [a]	3.19	x^2, y	0.46	0.207	0.390
Vryburg2 (n = 55)											
Brachymeria	**12.47*****	0.018	52.3 [a]	32.2 [c]	45.2 [b]	49.6 [a]	0.09	-	0.09	0.242	0.294
P. semitestacea	0.38	0.005	55.1 [a]	46.6 [b]	43.1 [c]	55.2 [a]	0.34	x^2	0.20	0.092	0.343
All species	2.01	0.012	80.1 [a]	58.9 [c]	66.5 [b]	80.0 [a]	0.26	-	0.26	0.253	0.329

Table 4. continued

Site (sample size)	1.	2.				3.	4.		5.	
	F statistic	slope	% Deviance explained (DE)				% DE	Spatial terms	% DE by host density	*X*	Max. simul. value
			Linear	Exp	Log	Power					
Gabane (generation 1, n = 60)											
Brachymeria	1.34	0.004	47.0 [a]	48.3 [a]	25.8 [b]	50.5 [a]	**10.46**(-)**	x^2	3.32	0.071	0.291
P. semitestacea	**5.84***	0.007	50.0 [a]	38.0 [b]	33.0 [b]	50.4 [a]	2.85	-	2.85	**0.307*****	0.269
All species	2.55	0.007	66.6 [a]	59.9 [b]	42.9 [c]	68.5 [a]	**11.37**(-)**	x^2, y	2.24	-0.112	-0.371
Gabane (generation 2, n = 56)											
Brachymeria	**15.00*****	0.014	66.2 [a]	43.5 [c]	55.5 [b]	63.5 [a]	0.55	-	0.55	-0.036	-0.345
P. semitestacea	**4.95***	0.008	54.1 [a]	44.9 [b]	37.2 [b]	56.7 [a]	5.26	-	5.26	**0.418*****	0.305
All species	**9.44****	0.017	81.3 [a]	79.3 [b]	78.3 [c]	82.3 [a]	**7.55*(-)**	-	**7.55*(-)**	**0.307***	0.525
Kumukwane (n = 51)											
?Tachinidae sp.	0.37	-0.008	21.8 [a]	22.3 [a]	23.0 [a]	21.9 [a]	4.98	-	4.98	0.180	0.371
P. semitestacea	0.00	0.000	14.5 [a]	14.6 [a]	14.9 [a]	14.5 [a]	1.43	-	1.43	0.307	0.347
All species	1.08	-0.019	36.1 [a]	32.7 [a]	33.0 [a]	36.2 [a]	3.64	-	3.64	0.210	0.369
Kopong (n = 38)											
P. semitestacea	0.67	0.031	17.9 [a]	15.3 [a]	19.2 [a]	17.5 [a]	0.02	-	0.02	**0.453*****	0.348
All species	3.11	0.071	37.9 [a]	24.5 [b]	43.3 [a]	34.4 [ab]	0.04	-	0.04	**0.581*****	0.399

Underlined values indicate loss of significance after column-wide step-up false discovery rate correction (at α=0.05) (García 2004). The large difference in the % deviance explained between methods 2 and methods 3 and 4 is attributable to the necessarily positive relationship between number of parasitised and total hosts (method 2), being taken into account by expressing number of parasitised hosts as a proportion of the total number of hosts in method 3 and 4.

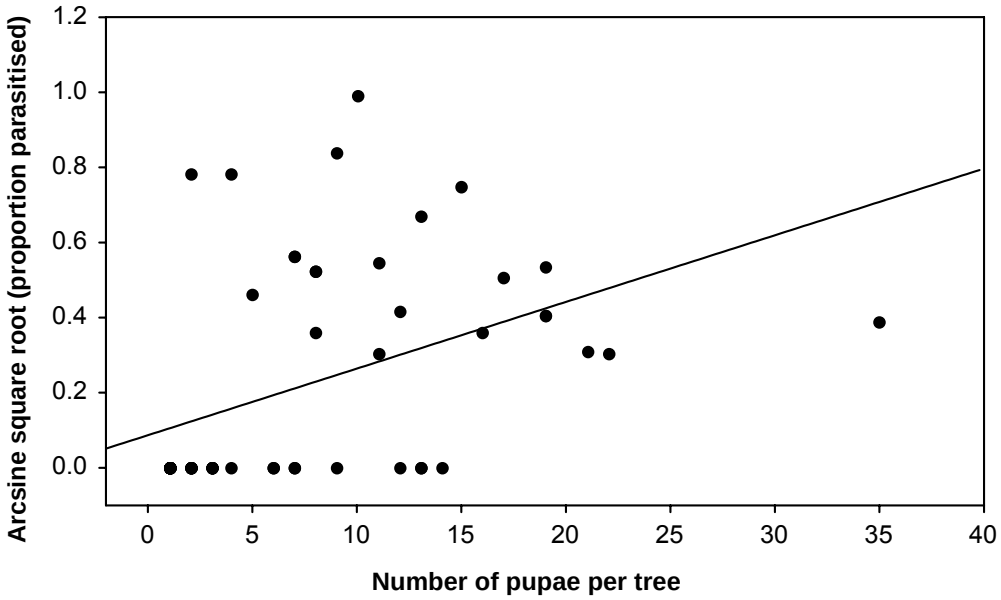

Figure 1. Arcsine square root method: transformed proportion pupae parasitised by *Brachymeria* sp. at Vryburg 2 positively related to pupal density (number of pupae per tree). The quantified linear relationship was weak (R^2 = 19.04%), indicating that the linear fit .should be interpreted with caution.

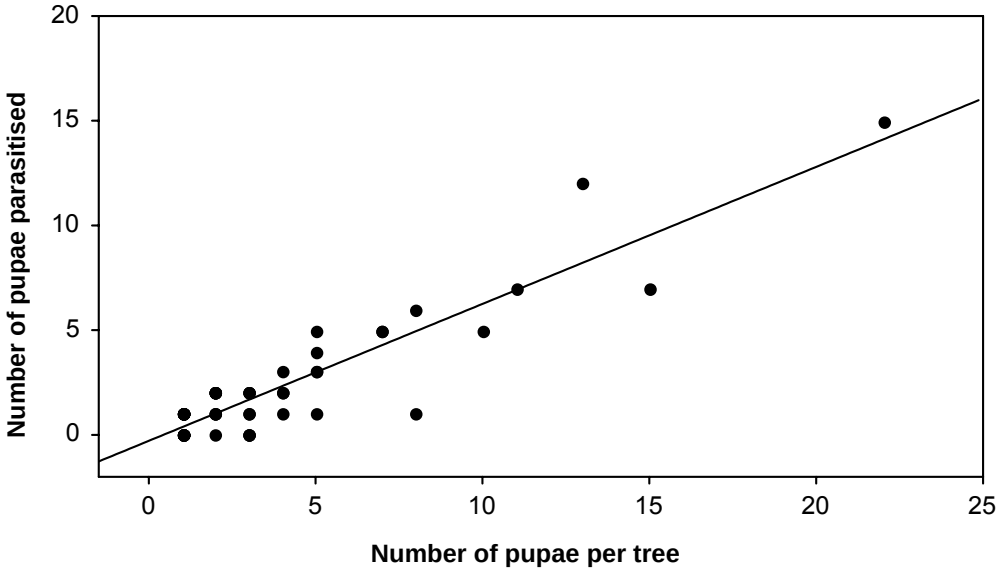

Figure 2. Regression function comparison: number of pupae parasitised by ?*Palexorista* sp. at Vryburg 1 with a constant positive relationship with pupal density. See Table 4 for strength and significance of depicted relationship.

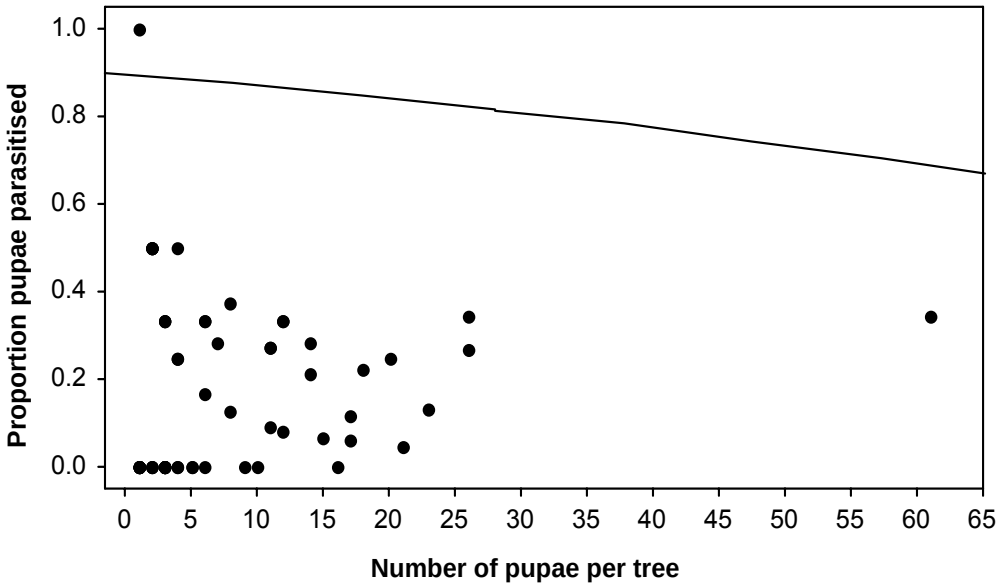

Figure 3. Binomial regression: proportion of pupae parasitised by all parasitoid species at Gabane (generation 1) determined by binomial regression with a negative relationship with pupal density. The quantified negative relationship was very weak (% deviance explained [%DE] = 11.37%), indicating that the slope .should be interpreted with caution.

Spatially associated density dependence

Spatial association identified six cases in which parasitism rate was significantly spatially associated with pupal density (Table 4). In all six cases of spatially associated density dependence the relationship was direct (positive) and in four cases highly significant (e.g. Fig. 4). Spatial association was not limited to certain localities, with usually at least one case (e.g. one parasitoid species) of significant positive association present at each locality. In three out of five cases the parasitism rate of *Pimelimyia semitestacea* was significantly associated with the number of available pupae (Table 4). By contrast, the parasitism rate of *Brachymeria* sp. was never (three cases) spatially associated with pupal density. Considering all parasitoid species at each locality together, significant spatial association was present twice. However in both cases *P. semitestacea* parasitism rate was spatially associated at the same site.

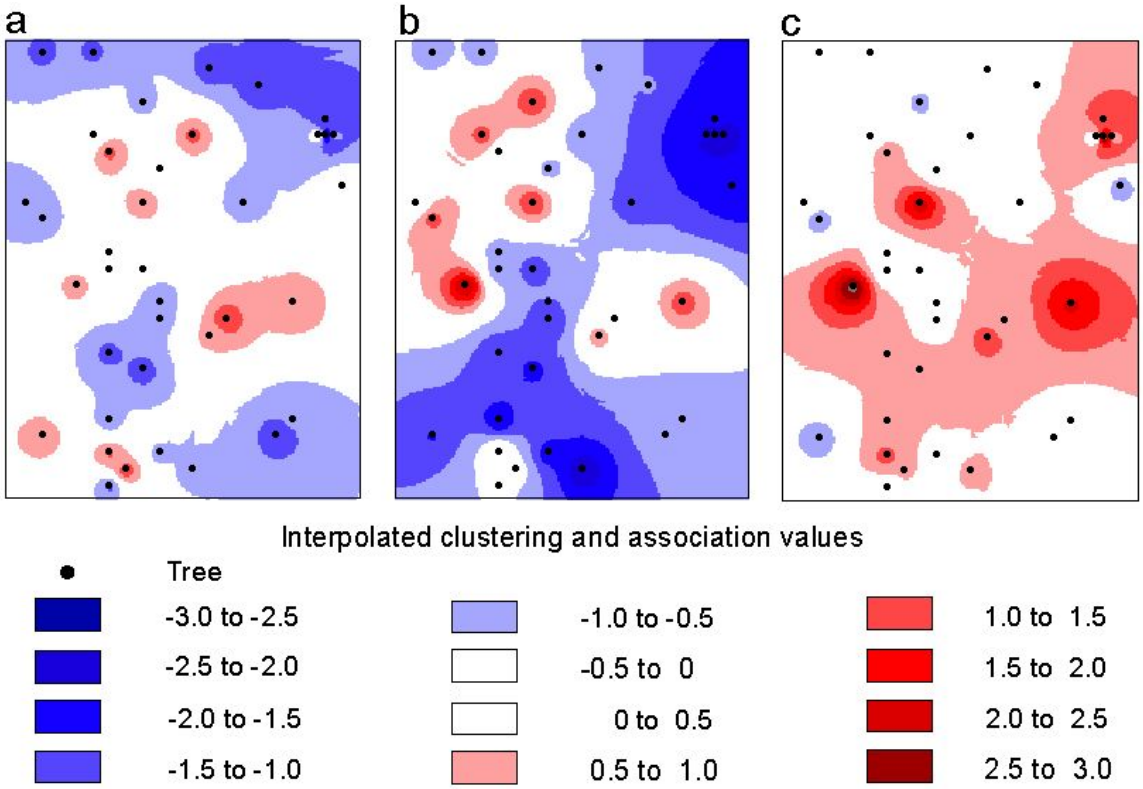

Figure 4. Example of method used to detect spatially associated density dependence. Interpolated (least distance weighted, Perry *et al*. 1999) spatial clustering and spatial association of wild silk moth pupae and parasitism rate by the fly, *Pimelimyia semitestacea*, on trees at Kopong. a) Spatial clustering of pupae (I_a = 0.94; p > 0.05). b) Spatial clustering of *P. semitestacea* parasitism rate (I_a = 1.16; p > 0.05). In both a. and b. areas coded > 1.5 denote areas of significant positive, and areas < -1.5 areas of significant negative, clustering. c) Spatial association between number of pupae and *P. semitestacea* parasitism rate (X = 0.453; p < 0.001). Areas coded as > 0.5 are significantly positively associated at the between-patch scale, while those < -0.5 are significantly negatively associated (Winder *et al*. 2001).

The results of the five methods were thus markedly different, not only in the prevalence of density dependence identified, but also in the sign of significant relationships. Spatial association identified significant density dependence in three instances where relationships were not significant using the other methods (Table 5). By contrast, the regression function

Table 5. Summary of patterns of density dependent (DD) parasitism shown by *G. postica*'s pupal parasitoids using spatially non-explicit methods (1-4) and a spatially explicit method (SADIE association test). 'ind', 'dir' and 'inv' refer to independent, direct, or inverse density dependence respectively. '?' indicates where the type of density dependence could not be determined. 'ns' non-significant after false discovery rate correction (García 2004). * indicates a poor fit (R^2 or %DE < 22%); while (+),and (+++) indicate weak and strong DD respectively.

Site	Parasitoid species	Spatial DD				Spatially associated DD
		1. Arcsine square-root	2. Regression function comparison	3. Binomial regression	4. Binomial regression with spatial terms	5. Spatial association
Vryburg1	?*Palexorista* sp.	ind	ind	ind	ind	dir (ns)
	All species	ind	ind	ind	ind	ind
Vryburg2	*Brachymeria* sp.	dir (+)*	? (not inv)	ind	ind	ind
	P. semitestacea	ind	ind	ind	ind	ind
	All species	ind	ind	ind	ind	ind
Gabane (gen 1)	*Brachymeria* sp.	ind	ind	inv (+)*	ind	ind
	P. semitestacea	dir (ns)*	ind	ind	ind	dir (+++)
	All species	ind	ind	inv (+)*	ind	ind
Gabane (gen 2)	*Brachymeria* sp.	dir (+)*	ind	ind	ind	ind
	P. semitestacea	dir (ns)*	ind	ind	ind	dir (+++)
	All species	dir (+)*	ind	inv (ns)*	inv (ns)	dir (ns)
Kumu-kwane	?Tachinidae sp.	ind	?	ind	ind	ind
	P. semitestacea	ind	?	ind	ind	ind
	All species	ind	?	ind	ind	ind
Kopong	*P. semitestacea*	ind	?	ind	ind	dir (+++)
	All species	ind	? (not dir)	ind	ind	dir (+++)

comparison was least sensitive to density dependence, with all relationships identified as density independent. All three significant standard binomial regression relationships were inversely density dependent (however, when including spatial terms, the contribution of host density became non-significant for two of these), and two of these were not identified as significant by the other methods. The arcsine square root method and spatial association were unique in being the only methods that identified direct density dependence. However, these two methods only shared three cases of direct density dependence.

Due to the marked differences between methods in detecting density dependence, only density dependence identified by spatial association is considered valid because of its advantages over traditional, spatially non-explicit approaches. Of *G. postica*'s parasitoids, two Tachinidae species, *P. semitestacea* and ?*Palexorista* sp., were the only parasitoid species that caused density dependent parasitism. *Brachymeria* sp. and the unknown Tachinidae species never resulted in density dependent parasitism.

DISCUSSION

The five methods used to detect density dependence in the parasitism rates of *Gonometa postica*'s parasitoids did not give similar results with regard to the form of density dependence detected. The spatially explicit method, spatial association, which uses more of the biological relevant information than traditional spatially non-explicit methods, is consequently regarded as the superior method of analysing density dependence in parasitism rates. Only spatial association indicated that *Pimelimyia semitestacea* repeatedly resulted in direct density dependent parasitism rates. Therefore, if this method was not used, the potential importance of this parasitoid for *G. postica* population dynamics (Chapter 1) would not have been correctly predicted.

Spatial association revealed that density dependence was usually weak at the site scale, and only indicated strong density dependence at isolated trees within a site. The magnitude of the strongest relationship quantified at this scale, using overall spatial association, was 0.58, while the theoretical maximum is 1.00. This confirms that the density dependence in pupal parasitism rates were relatively weak in this study. Nonetheless, overall association values of

positive relationships in biological data usually range between 0.05 and 0.60 (Thackray *et al*. 2002), and 0.7 may represent a biological realistic maximum in ecological associations. For example, it is generally accepted that R^2 values of 70% indicate a very strong relationship in ecology. An overall association value of 0.58 is thus in fact very large. However, local association values were significant (2.5 and greater), for only a few single trees. Thus, the strength of density dependent parasitism observed in *Gonometa postica* populations is highly variable at the site scale, i.e. between trees. No other method was able to provide information on the pattern of density dependence in such spatial detail.

Two biological reasons for density independent parasitism rates have been proposed. First, analysing the spatial pattern of parasitism of more than one parasitoid species simultaneously might obscure the detection of density dependent parasitism (Heads & Lawton 1983). In this study, *P. semitestacea* and ?*Palexorista* sp. were the only parasitoid species to show spatially explicit density dependence. Combinations of all parasitoid species rarely exhibited spatially associated density dependence, even if specific species on their own were found to be density dependent. Therefore, when parasitism rates of different parasitoid species are lumped for analyses (Williams *et al*. 2001) or are indistinguishable (Heads & Lawton 1983), the true type of density dependent relationship between individual parasitoid species and their host may thus be obscured. Second, density independent parasitism rates may be due to sequential parasitism. Lessells (1985) previously illustrated how direct density dependence may be missed when different parasitoid species parasitise the host sequentially. In this study it may be the case as *P. semitestacea* is suspected to parasitise final instar larvae first and other parasitoid species to follow thereafter. This may be a plausible explanation for why density dependence was only detected for this species.

Another potential reason for the form of density dependence detected is the scale of investigation (Heads & Lawton 1983; Ray & Hastings 1996). In this study all tests for density dependence were conducted at the between-plant scale. It has further been suggested that density independent parasitism rates will be the norm for insect herbivores varying in abundance at the between-plant scale (Norowi *et al*. 2000). However, this study found both density dependence and density independence in parasitism rates when using the same parasitoid species and method. This suggests that scale is not responsible for the form of density dependence identified at the between-plant scale in this study.

However, as illustrated by this study, the method used can also severely affect the form of density dependence detected. Traditional (spatially non-explicit) methods of detecting density dependence may be especially prone to missing significant density dependence when attack rates are below 10% and the host's abundance is low (Trexler *et al*. 1988). Generally, and as found in this study, curve fitting methods perform especially poorly, not being powerful enough to distinguish the form of density dependence (Trexler *et al*. 1988; McGill 2003). Binomial regression, on the other hand, tends to indicate density independence much more often than density dependence and, in the latter, usually weak inverse density dependence is detected (Hails & Crawley1992; Norowi *et al.* 2000; this study). Therefore, when using binomial regression, although host density may account for some variance in the proportion of parasitised hosts, this amount is usually small. A large proportion of parasitism risk is thus not accounted for by host density (e.g. Norowi *et al.* 2000, and this study). The high probability of making a Type II error when using this method, limits it value in detecting density dependent parasitism under field conditions, which are likely to be weak (see also Hails & Crawley1992). In contrast, spatial association does not violate statistical assumptions of spatial independence, incorporates what is known to be biologically relevant spatial information in host abundance, and is more sensitive (has greater power; Winder *et al*. 2001) to the detection of weak density dependent relationships, it offers an advantageous alternative to traditional methods. Thus, using a spatially explicit method of detecting density dependence is not similar to using spatially non-explicit methods.

The explicit inclusion of spatial information in ecological models is being increasingly adopted (Legendre *et al.* 2002; Perry *et al.* 2002), although it is still rare in analyses of density dependence (e.g. Dolman & Sutherland 1997; Hassell 2000; Berryman 2003). In two examples (Roland & Taylor 1997; Loch & Zalucki 1998) where spatial referenced data are used in density dependent (parasitism) investigations, spatial information was not used in the quantification of aggregation in host abundance and the spatial pattern described was not location-specific. Trend surface analysis (Roland & Taylor 1997) or testing for spatial autocorrelation in parasitism rate (Roland & Taylor 1997; Loch & Zalucki 1998) is an incomplete solution, because although it accounts for the spatial variance or the spatial structure in parasitism rate, it does not quantify the spatial relationship with host abundance. In this study, in the absence of spatial autocorrelation in host abundance (see Chapter 3), spatial

association was still able to match isolated (single sample point) areas of high host abundance and high parasitism rate.

The value of using spatially explicit abundance data to investigate insect predator-prey cycles (by determining spatial association over time) has been illustrated previously (Bohan *et al*. 2000; Ferguson *et al*. 2000; Winder *et al*. 2001). In these studies delayed temporal density dependence is inferred from quantifying the degree to which predator densities temporally track prey densities. No studies to date have, however, investigated the spatially explicit relationship between host density and mortality rate, allowing a direct test for the presence of spatially explicit (associated) density dependence. Using *Gonometa postica* and its parasitoids as a case study, we have illustrated that spatial association between host abundance and parasitism rate measured in one generation can be used to detect spatially-explicit density dependence. By defining spatial patchiness in the most biologically relevant manner (Perry 1998), the search for spatial density dependence was made more powerful.

The results of this study show that the degree of spatial explicitness determines if, and what form, of density dependence is detected. This has implications for decades of work on the detection of density dependence in parasitism rates of insect herbivore parasitoids (1941-1987, reviewed by Stilling 1987, and Walde & Murdoch 1988). In these studies the spatially explicit pattern of host abundance (position of sample points and neighbours) was not considered. By omitting spatial data the frequency of density dependent parasitism may have been underestimated. Although studies on density dependent parasitism refer only to patterns in mortality and not to the processes that cause them, exploring the use of spatial explicit data in other HPR's (e.g. population functional response, see Table 1) may provide further insight into processes that lead to density dependence. Furthermore, the quantification of the density dependence in parasitism rates has been, and still is, an important topic in host-parasitoid population dynamics (Hassell 2000; Haak 2002). Natural enemies are thought to only regulate prey populations when they induce density dependent mortality (Crawley 1992). Density dependence has thus profound implications for our current understanding of population regulation.

The fact that markedly different conclusions on the prevalence and form of spatial density dependence are reached with alternative methods, calls for a re-evaluation of its statistical definition. In summary, spatial association does not violate statistical assumptions of

spatial independence, incorporates biologically relevant spatial information on host density and parasitism risk, and has greater power to detect weak density dependent relationships than other methods (Winder *et al*. 2001; Perry & Dixon 2002). This method is thus the superior method for detecting spatial density dependent parasitism or other relationships. While the debate on the consequences of density dependence for host population dynamics continues (Godfray & Hassell 1997; Berryman 2003), the statistical definition and quantification of density dependent relationships remain fundamental to the field of population ecology (Haak 2002). Given that density dependent processes form part of all five of the so-called 'principles' of population ecology (geometric growth, cooperation, competition, interacting species and limiting factors; Berryman 2003), the ability to detect density dependence, in general, is an issue of vital importance.

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