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SHORT COMMUNICATION

SPREAD OF THE WASP PARASITOID *SPHECOPHAGA VESPARUM VESPARUM* FOLLOWING ITS RELEASE IN NEW ZEALAND

Summary: The measurement of parasitism rates of wasp nests at Pelorus Bridge, New Zealand, at different distances from the initial release point suggests that the mean displacement of the parasitoid has increased by 1 - 1.5 km y^{-1} from 1988 to 1993. Since average parasitism rates within this radius at any given site show little trend over time, this suggests an approximate 3-fold increase in the total parasitoid population each year, two-thirds of which is devoted to dispersal and one-third to maintaining local populations.

Keywords: Wasp, parasitoid; *Sphecophaga vesparum vesparum*; *Vespula vulgaris*; *Vespula germanica*; spread; dispersal; New Zealand.

Introduction

The parasitoid *Sphecophaga vesparum vesparum* (Curtis) (Hymenoptera:Ichneumonidae) was introduced as a possible biological control agent against wasps (*Vespula vulgaris* (L.) and *V. germanica* (F.)) in New Zealand (Donovan and Read, 1987), and released from 1987 onwards as overwintering cocoons. Releases took place at numerous sites throughout New Zealand (Donovan *et al*., 1989) and a total of 108,000 cocoons were distributed in the first three years (Read, Donovan and Schroeder, 1990). Since then, establishment has been confirmed at only two sites, both in the South Island: Pelorus Bridge, 25 km east of Nelson (Donovan *et al*., 1989; Thomas *et al*., 1990); and Ashley Forest, 50 km north of Christchurch (Beggs, Harris and Read, 1996). No parasitoids were recovered from 1190 nests at 38 other sites where they were released and monitored (Moller *et al*., 1991; Beggs *et al*., 1996).

This paper describes and quantifies the rate of spread of parasitoids outwards from the Pelorus Bridge release site, from 1987 and 1988 when they were released, until 1993.

Methods

Following parasitoid releases in 1987 and 1988, nests surrounding and within 10 km of the Pelorus Bridge release site were dug up each autumn from 1988 to 1993 and dissected to determine the presence and number of parasitoids (Beggs *et al*., 1996). In any given year, the outward displacement of the parasitoid was estimated as the weighted average of the radial distances to the middle of successive concentric annuli (rings) around the release site, the weighting in each case being an index of the proportion of dispersing parasitoids in that annulus (Fletcher, 1974; Southwood, 1981). This index was estimated as:

$$\textit{proportion in } i\textit{th annulus} \propto (\textit{area of } i\textit{th annulus} \times \textit{\% parasitism in } i\textit{th annulus}) / (\Sigma_{i=1}^{\infty} \textit{area of } i\textit{th annulus} \times \textit{\% parasitism in } i\textit{th annulus})$$

If one or more parasitised nests were found in an annulus which had few nests dug in total, the results were pooled with those of an adjacent annulus in order to give a total of at least 10 nests before calculating the dispersal distance. The annuli were 0.2 km wide up to 2 km from the release site then 0.5 km wide thereafter (see Table 1). Aggregating the data and annuli into fewer groups with larger total numbers of nests in each had little effect on the resulting estimates of mean displacement. Percentage parasitism is analogous to recaptured insects per trap in Southwood's (1981) description of the method, so long as the density of wasp nests within each annulus is constant. In the absence of evidence to the contrary and in view of the broadly similar densities found throughout *Nothofagus* forests in the area (Barlow, Moller and Beggs, 1996), this was assumed to be the case. The other major caveat is that the full outward displacement of the parasitoid is encompassed within the annuli searched, since recoveries in the furthest annuli contribute particularly significantly to the weighted average distance (Southwood, 1981).
It is unlikely that this condition was met, particularly in the last few years of the study, so estimates of mean parasitoid dispersal distances will be conservative.

Results

Table 1 shows the number of nests dug up and the number of these parasitised at different distances from the release site from 1988 to 1993, and Table 2 gives an example of the calculation for the mean displacement of the parasitoid in a particular year, in this case 1990. Calculated in this way, the mean displacement increases approximately linearly with time, thus (Fig. 1):

[*Displacement*] = -1.32 + 1.15[*Years since 1987*]
$R^2 = 0.63$, $d.f. = 4$, $p = 0.038$

There is a suggestion from Fig. 1 that the rate of spread (i.e., the slope of the line) initially increases with time, before a steady state is reached. Thus, omitting the first year (1988) from the relationship gives a slightly greater slope of 1.37 (compared with 1.15) and omitting the first two years gives a slope of 1.59. Both these latter relationships between displacement and years are statistically non-significant (p>0.05). However, they simply represent best estimates of the parasitoid's rate of spread from the data available. Overall, the data suggest a velocity of spread of around 1.15 - 1.6 km per year. This contrasts with the maximum distances from the release site at which parasitoids were recovered, which represent the extreme 'front' of expansion but are unreliable measures of the rate of spread because

Table 1: *Wasp nests dug (N) and number of these parasitised (N_p) at different distances from the Pelorus Bridge release site, from 1988 to 1993.*

Annulus	Distance (km)	1988 N	1988 N_p	1989 N	1989 N_p	1990 N	1990 N_p	1991 N	1991 N_p	1992 N	1992 N_p	1993 N	1993 N_p
1	0.0-0.2	22	1	79	8	101	5	32	0	92	22	56	7
2	0.2-0.4	5	0	20	2	17	0	29	2	31	5	38	3
3	0.4-0.6	8	0	39	0	21	1	21	0	44	9	21	2
4	0.6-0.8	2	1	7	0	21	2	30	3	40	4	54	2
5	0.8-1.0	0	0	1	1	7	0	30	1	12	1	24	2
6	1.0-1.2	0	0	2	0	3	1	9	0	10	1	7	0
7	1.2-1.4	2	0	8	0	2	0	3	0	11	0	4	0
8	1.4-1.6	0	0	9	0	1	0	21	0	17	0	7	0
9	1.6-1.8	2	0	22	0	5	1	0	0	3	0	3	0
10	1.8-2.0	1	0	52	0	12	0	0	0	0	0	0	0
11	2.0-3.5	0	0	90	0	62	0	7	0	11	1	24	0
12	3.5-5.0	0	0	12	0	13	0	19	0	13	0	15	0
13	5.0-6.5	0	0	0	0	0	0	13	0	53	1	16	0
14	6.5-8.0	0	0	4	0	39	1	30	0	52	1	65	5
15	8.0-9.5	0	0	13	0	70	0	10	0	39	0	2	0
16	>9.5	0	0	0	0	0	0	0	0	30	0	17	0
Mean parasitoid displacement (km)		0.58		0.82		2.89		0.68		4.25		6.98	

Table 2: *Example calculation of the outward displacement of the parasitoid by 1990. The distances to the near and far edges of the ith annulus are denoted by x_{i-1} and x_i respectively, the proportion of the total parasitoids that occurs in each annulus is estimated from the percentage parasitism of wasp nests in this and all other annuli as $Q_i = P_iA_i / SP_iA_i$ and in this case SP_iA_i is 27.76. Mean displacement of parasitoid = SQ_iD_i = 2.89 km.*

Annulus	Location of annulus	Parasitism (P_i, %)	Area index $A_i = x_i^2-x_{i-1}^2$	Proportion of parasitoids (Q_i) $D_i = (x_i+x_{i-1})/2$	Distance (km) $D_i = (x_i+x_{i-1})/2$
1	0.0-0.2	4.95	0.04	0.0071	0.1
3	0.4-0.6	4.76	0.20	0.0343	0.5
4	0.6-0.8	9.52	0.28	0.0960	0.7
6	0.8-1.2*	10.00	0.80	0.2882	1.0
9	1.6-2.0*	5.88	1.44	0.3050	1.8
16	6.5-8.0	2.56	2.92	0.2693	7.3

**based on pooled annuli giving a total of at least 10 nests (compare with original data for 1990 in Table 1).*

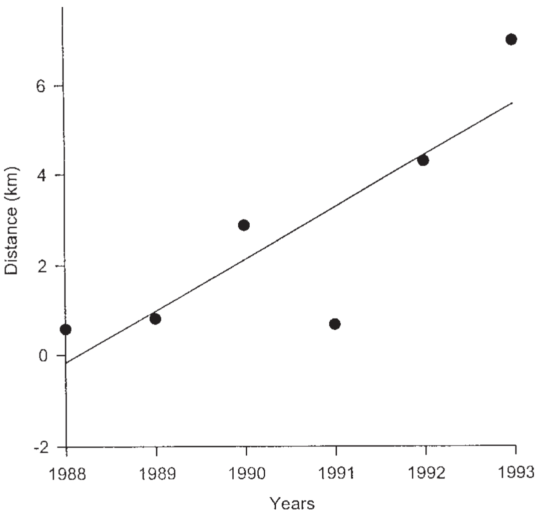

Figure 1. *Cumulative mean displacement of the parasitoid population from the release site, plotted against the year (release was in 1987). Points are based on the calculations illustrated in Table 2 and the line is: [Distance] = -1.32 + + 1.15[Years since 1987].*

they are based on such small numbers. Thus, the furthest distance at which parasitoids were recovered reached 7.3 km by 1990, dropped to 0.9 km in 1991 then rose to 7.3 km again in 1992 and 1993 (Table 1).

The rate at which the parasitoid spreads implies a certain rate of increase in the total population, as opposed to the observed rate of increase at any one site within the existing range, which is quite low (see below). Table 3 shows the derivation of an index of the total rate of increase, based on estimates of the number of parasitised nests enclosed by a boundary represented by the mean displacement.

Table 3: *Estimation of an index of the total population of parasitised nests in successive years, based on the mean displacement (see text and Table 2), the proportion of wasp nests parasitised within this boundary (from Table 1), and the wasp nest density (Beggs* et al.*, 1996).*

Year	Estimated mean displacement (km)	Nest parasitism rate within mean displacement	Wasps nests per ha	Total parasitised nests within mean displacement
1988	0.58	0.054	10.5	60
1989	0.82	0.033	15.8	110
1990	2.89	0.040	8.2	861
1991	0.68	0.030	11.6	51
1992	4.25	0.159	12.1	10917
1993	6.98	0.063	23.8	22950

This index should be proportional to the total parasitoid population, and can therefore be used to estimate the global rate of increase. Regressing the natural logarithm of the total population index (last column in Table 3) against time gives a relationship:

$$Ln\ [parasitised\ nests] = 2.40 + 1.16\ [years\ since\ 1987]$$

$R^2 = 0.57$, $d.f. = 1,4$, $p = 0.05$

The relationship is linear, which indicates an exponentially growing total population with an annual specific rate of increase of 1.16. The ratio of increase per year is therefore $exp(1.16) = 3.2$, and since there was no significant increase in parasitism locally (Table 3), this implies that about two-thirds of the parasitoid's potential for increase over the years 1988 - 1993 was devoted to spread and colonisation of new habitat, compared with one-third to maintenance of local populations.

Discussion

The approximate linearity of the displacement/time relationship in Fig. 1 is consistent with a theoretical population subject to diffusive (i.e., density-independent, or proportional) movement and exponential local growth. For such populations, the radius of the area they occupy increases linearly with time, whereas for populations dispersing without reproduction, the area rather than its radius increases linearly with time (e.g., Skellam, 1951; Okubo, 1980). The latter would translate to a decreasing velocity of expansion over time, and there is no theoretical basis for a continually increasing velocity of radial expansion with time. On the other hand, a reaction-diffusion model involving exponential population growth and diffusive dispersal does predict an initially increasing velocity of expansion until a steady state is reached, and there is a suggestion of this in Fig. 1.

The observed local rate of increase in nest parasitism at Pelorus Bridge has been slow or non-existent. Plotting the natural logarithm of the estimated number of parasitised nests per hectare within 2 km of the release site against time, from 1988 to 1993, gives a slope of 0.246. Although this is statistically non-significant because of the variability from year to year, it does suggest that the local, as opposed to global, rate of increase is between 0 and 0.246 y^{-1}, or a 1 - 1.3-fold ratio of increase y^{-1}. The carrying capacity, or local equilibrium level for the parasitoid also appears to be low, in the sense that only about 10% of available *Vespula* nests are actually parasitised (Barlow *et al.*, 1996).

In conclusion, the rate of spread of 1 - 1.5 km per year suggests that *S. vesparum vesparum* has a moderate dispersive ability, though there are few other examples in the literature with which to compare it. *Aphytis melina* DeBach released in Greece to control scale insects spread at about 100 km y^{-1} (DeBach and Argyriou, 1967), while the aphelinid *Cales noacki* Howard colonised an area of 80 km^2 in eighteen months in France (Onillon, 1990). At the other extreme is the aphelinid *Encarsia lahorensis* (Howard), which moved only 1600 m in 10 years in Florida (Onillon, 1990), and the braconid *Agathis pumilla* (Ratz.), which spread at a rate of approximately 100 m per year in Montana and Idaho (Long, 1977). These estimates are much more approximate, and not strictly comparable with, that obtained in the present study. The rate of increase in the area covered by *S. vesparum vesparum* implies a 3-fold increase in total population each year at Pelorus Bridge, of which about two-thirds is devoted to colonisation of new habitat and one-third to maintenance of local population density. The high global rate of population growth thus contrasts with a very low local rate of increase and/or carrying capacity relative to the host's abundance: the parasitoid population seems to spread at a moderate rate but be incapable of significant growth. There is no reason to suppose that its performance would differ elsewhere in New Zealand, and it is the apparent low local equilibrium level and/or slow rate of local increase, rather than poor dispersive ability, which is likely to limit its future impact as a biological control agent of wasps.

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