Eur. J. Entomol. **93**: 319–324, 1996
ISSN 1210-5759

An altitudinal transect as an indicator of responses of a spittlebug (Auchenorrhyncha: Cercopidae) to climate change

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Auchenorrhyncha, Cercopidae, *Neophilaenus lineatus*, spittlebug, altitude, climate change

Abstract. A projected global temperature rise of 2–3°C can be represented by the change in mean annual temperature experienced over some 10° of latitude or approximately 700 m of altitude in the hills of northern Britain. Using an altitudinal rather than latitudinal transect has the advantage of allowing studies of population dynamics and adaptation of life cycles at the centre and edge of a species' range within the same locality with similar vegetation and photoperiod.

Because of their unusual visibility in spittle masses, spittlebugs offer unusual opportunities to study population change in relation to environmental variables, including climate change.

A population of spittlebugs, *Neophilaenus lineatus* (Auchenorrhyncha: Cercopidae) has been studied for 10 years on a transect from 20 m to 974 m on Ben Lomond, Scotland. The time lag in larval development corresponding with a 2–3°C shift in mean temperature is approximately 3 weeks. Much of this arises from a delay in hatching times. There is a significant relationship between the weather in March to July (which spans hatching and early larval development) and the maximum altitude at which larvae are found in the same year. The study suggests that insects with a similar life cycle to *Neophilaenus lineatus* will respond to a 2°C rise in mean temperature by extending their range and completing the life cycle two to three weeks earlier.

INTRODUCTION

Although a completely secure link between greenhouse gases and global warming still eludes us (Anonymous, 1994) it is generally accepted that a mean rise in temperature of some 2–3°C is likely to take place over the next 50 to 60 years (Houghton et al., 1990). If this should occur, it is important that we have models enabling us to predict the likely consequences to populations of plants and animals. It is extremely difficult and probably misleading to try to do this solely from laboratory information about responses to temperature change, because there are potentially so many confounding factors in the field. These also make predictions based on data from latitudinal transects in the field suspect, because it is rarely possible to compare populations along transects on which temperature is the only or main variable. A transect of some 800 miles in length would be required to simulate the expected rise in temperature. Over such distances, natural enemies, vegetation and particularly photoperiod would be important variables. We have therefore argued (Butterfield et al., 1991) that altitudinal transects are much more practical for this purpose. An increase in altitude of 100 m entails a fall in mean temperature of approximately 0.6 to 0.7°C (Pearsall, 1950) so that a projected rise of 2°C is to be expected over an altitudinal gradient of some 300 m. Such a distance is easy to access for repeated detailed sampling of natural populations and can be found on the same vegetation type and with no change in photoperiod. This paper describes one such study in which the temperature lag along a montane transect is used as an open air laboratory to study effect of temperature change in the field on development rates and distribution of an insect.

STUDY SITE, MATERIAL AND METHODS

We have been studying a number of insect species on montane transects in northern England and in Scotland. Here we will concentrate on one transect on the mountain Ben Lomond in Stirlingshire, Scotland (Nat. Grid NN367029) and on the spittlebug *Neophilaenus lineatus* (L.) (Auchenorrhyncha: Cercopidae). The presence of highly visible spittle around the nymphs of this species makes it easy to sample at all altitudes in all weather conditions and data are available for 10 consecutive years. *N. lineatus* has 5 larval instars which are all protected by spittle masses; by-products of feeding on grasses and rushes (Whittaker, 1965, 1971). It is possible to identify these stages in the field. Hatching is normally in early May in the lowlands and adult emergence takes place some 6 weeks later (Whittaker, 1971). Ben Lomond (974 m) was visited on or about (± 2 days) the first of July from 1986 to 1995. In 1995, the mountain was also visited on 5 occasions between May and August. There is continuous similar vegetation (*Juncus squarrosus* and *Nardus stricta*) available as food plants throughout most of this transect, except at the lowest two stations. On each visit, samples of the larvae were collected at a minimum of 4 stations (usually 5) at approximately 150 m intervals up a transect from 20 m a.s.l. to as high as the larvae could be found on the mountain. In some years this was as low as 530 m and in others as high as 900 m. We are satisfied that we could find the larvae if present, because in 1993 and 1994, for example, those at the top of the transect were readily found in instars one and two when the spittles are smallest. The instar composition of the population was determined at each station usually from a minimum of 40 individuals per station (except in a few cases where this number could not be found). On one occasion (1–3 July 1995), five separate samples were taken at the 520 m station, each of not less than 40 individuals to check that this number was sufficient to give an accurate picture of the true instar composition. There were no significant differences in instar composition between the 5 samples ($\chi^2 = 0.8$; 2 d.f., $P > 0.95$) and so it was concluded that the sample size was adequate. A simple index of instar development was calculated by the method of Hodkinson et al. (1979) in which the index shows the mean stage of development of instars 1–6, where 1–5 are larvae and 6 is the adult. This index is only directly related to development rate after stage one has been concluded and before stage 6 is reached, since the relationship is sigmoid.

RESULTS

Table 1 records the instar composition of larvae of *N. lineatus* on or about 1 July on Ben Lomond from 1986 to 1995. The extent to which larval development is retarded with altitude may be seen (Fig. 1). In 1994 for example, 98% of larvae had reached instar 5 (mean 4.98) at 90 m a.s.l. whereas at 530 m (the maximum altitude at which larvae were found in that year) stage one could still be found (mean 2.1). Thus a change of altitude of some 440 m resulted in retardation of development of about 2.8 instars. At a lowland site such as Wytham Woods, Berkshire, England, this would be the equivalent of about 5 weeks of development (Whittaker, 1971). This lag in development of *N. lineatus* may be caused by a delay in hatching date with altitude and/or slower development from hatching to the time when the samples were taken. Our data from 1995 when samples were taken throughout

TABLE 1. Instar composition of *N. lineatus* on or about 1 July in 1986 to 1995 on an altitudinal transect from 20 m to 974 m on Ben Lomond, Scotland.

Year	Alt. (m)	Larval and adult instar (%)						Total n	Index*
		1	2	3	4	5	Adult		
1986	540			47	53			17	3.5
	395			23	77			43	3.8
	240			8	71			21	4.1
	90				15	85		61	4.9
1987	680			67	33			3	3.3
	570			32	68			28	3.6
	365				50	50		44	4.5
	200					100		25	5.0
1988	900		38	62				42	2.6
	810		2	90	8			62	3.1
	600			9	88	3		58	3.9
	300					100			5.0
1989	780		16	84				38	2.8
	580			62	26	12		58	3.5
	390			6	38	55		65	4.5
	200			4	7	89		73	4.9
1990	820			62	38			21	3.4
	600			11	80	9		56	4.0
	400				10	88	2	68	4.9
	210				2	88	10	50	5.0
1991	740		3	30	60	7		60	3.7
	660		4	6	87	2		47	3.9
	540			5	55	40		58	4.3
	330				2	98		51	5.0
	150					100		43	5.0
1992	880			47	53			57	3.5
	820			5	95			40	3.9
	760			22	78			50	3.8
	570				85	15		54	4.2
	410				4	96		50	5.0
	228					68	32	41	5.3
1993	720	8	25	67				12	2.6
	580		13	49	38			53	3.3
	425			4	72	23		47	4.2
	275				14	86		74	4.9
	125					89	11	27	5.1
1994	530	14	61	25				28	2.1
	378		4	55	41			44	3.4
	227			2	82	16		43	4.1
	91				2	98		49	5.0
1995	830			58	42			12	3.4
	680			17	73	10		63	3.9
	530				39	61		46	4.6
	370				2	98		44	4.9
	221					98	2	43	5.1
	84					97	3	31	5.4

* Index of development: $I = \sum_{i=1}^{6}(n_i \cdot i)/T$ (Hodkinson et al., 1979).

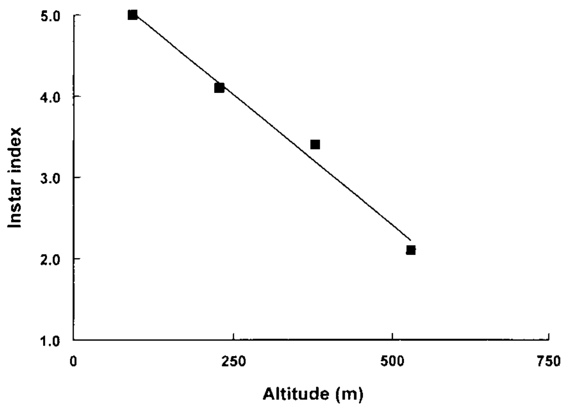

Fig. 1. Relationship between index of larval development (Instar index) and altitude on Ben Lomond on 1 July 1994.

the season show that the main cause of the lag is a progressive delay in hatching dates at higher altitudes. On 10 May, for example, hatching had not taken place at 330 m, but at 150 m 95% of the larvae were in instar one, and at 30 m 83% were in instar two and 9% in instar three. One month later, larvae found at 570 m were all in instar two. Thereafter, the effect of this lag is gradually reduced and this is reflected in the slopes of the regressions of instar indices on altitude (Table 2). At the beginning of the season shortly after hatching the slope is high indicating a large lag in development as altitude increases. Towards the end of the season (29 July), the slope is much less, indicating that larvae high up the mountain have caught up some of the lag resulting from late hatching. This matches the finding of Whittaker (1965) in his study of a population of *N. lineatus* on a transect in northern England.

TABLE 2. Slopes of regressions of index of development of *N. lineatus* on altitude at progressive dates in 1995 on Ben Lomond.

Date	Slope ± 1 SE
10 May	−0.0063 ± 0
10 June	−0.0037 ± 0.0013
3 July	−0.0022 ± 0.0004
29 July	−0.0016 ± 0.0005

An important feature of the data is the maximum altitude at which *N. lineatus* was found on Ben Lomond over the 10 year period. It varied between 530 m and 900 m (Table 1). There is a significant relationship ($r^2 = 0.89$; 8 d.f.; $P < 0.01$) between this altitude and mean maximum temperature from April to June, the months when larvae are hatching and growing. Fig. 2 shows that in years in which the mean temperature from March to June was warmer than the 25-year mean, the larvae were found higher up the transect and in years which were cooler than average during these months, the maximum altitude reached was depressed ($r^2 = 0.63$; 8 d.f.; $P < 0.01$).

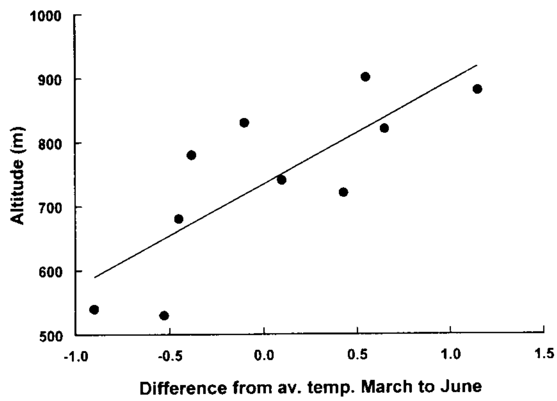

Fig. 2. The relationship between the difference from the 25 year mean average temperature from March to June in 1986 to 1995 and the maximum altitude of *N. lineatus* larvae on Ben Lomond on or about 1 July.

DISCUSSION

The temperature lag over the entire range of the transect on Ben Lomond (890 m) might be expected to be, on average, about 6°C. The predicted 2–3°C rise in mean temperature from global warming is equivalent to about 300 m of this transect. Thus a 2–3°C rise in the mean temperatures in the Ben Lomond area should result in populations on 1 July being at a stage hitherto found some 300 m further down the mountain side. It is essential (Whittaker, 1971) that *N. lineatus* adults emerge in time to complete egg development before autumn frosts prevent them from doing so. A 2–3 degree rise is therefore likely to ensure that this can happen up to 1050 m rather than up to about 750 m, the present average. Populations may therefore persist to this height and may disperse in the adult stage to even higher altitudes. There is evidence from pit-fall traps at 1000 m in the northern Pennine hills of England that *N. lineatus* adults may readily disperse to these heights without larvae normally being found there (J.C. Coulson, pers. comm.). However, the relationship between mean temperature in March and June with maximum altitude was unexpected and implies that even if warmer conditions in the previous summer and autumn encourage dispersal to higher stations up the mountain, whether the population actually persists there is much more dependent on the weather conditions at the time of hatching and establishment of larvae in the current year. Warmer conditions at this time are the key to the spread of the population upwards. The principal natural enemy of *N. lineatus*, the pipunculid *Verrallia aucta* (Whittaker, 1969) is not thought to have any influence on these findings since parasitised specimens have not been found above 250 m.

In summary, this study suggests that insects with a similar life cycle to *N. lineatus* will respond to a 2°C rise in mean temperature by extending their range and completing the life cycle some two to three weeks earlier.

In a further study we are attempting to discover whether similar considerations apply to geographical spread of the species along latitudinal transects and are also testing the effect of experimentally transferring individuals up and down montane transects, including moving them to stations above their present range to monitor the effect on development rates and survival. These will be reported elsewhere.

ACKNOWLEDGEMENTS. We are indebted to A.J.C. Malloch and 10 cohorts of Ecology students from Lancaster University who helped to collect the samples under the supervision of JBW, sometimes in difficult weather conditions. The study forms part of a programme funded in the TIGER initiative by the Natural Environment Research Council to whom we are very grateful for support.

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