

Life history and host-plant relationships of the rare endemic Arctic aphid *Acyrtosiphon calvulus* in a changing environment

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Accepted: 16 January 2007

Key words: *Salix polaris*, *Pedicularis hirsuta*, Spitsbergen, Svalbard, phenology, progeny, sex ratio, reproduction, survival, metapopulation, Homoptera, Aphididae

Abstract

This article examines the abundance, life history, host-plant relationships, and overwintering biology of *Acyrtosiphon calvulus* Ossiannilsson (Homoptera: Aphididae) as a precursor to understanding its rarity and potential response to a changing climate. *Acyrtosiphon calvulus* is restricted to a few scattered localities on the west coast of Spitsbergen, Svalbard, Norway, where it reproduces on *Salix polaris* WG (Salicaceae) and its taxonomically unrelated root parasite *Pedicularis hirsuta* L. (Scrophulariaceae). *Acyrtosiphon calvulus* overwinters as eggs. Hatching fundatrices give rise directly to males and oviparae, which mate and lay overwintering eggs. The life cycle is closely synchronized with the phenology of *S. polaris* and appears genetically programmed, lacking summer generations of viviparae. Alate forms are similarly unknown. The progeny sequence of fundatrices resulted in a sex ratio for the sexuales that is strongly female biased (3:1). Eggs hatch coincided with budburst in early June and fundatrices developed on the expanding leaves. Egg production by oviparae corresponded with leaf senescence in July and August. Overwintering egg survival was high, with supercooling points ranging from -29 to -40 °C, lower than the extreme winter minimum temperature recorded (-28 °C). Egg development and hatching occurred at or below 5 °C and sub-zero temperatures were not required to break diapause. The scarcity and fragmented distribution of *A. calvulus* is discussed in the context of the ubiquity of its host plants on Spitsbergen.

Introduction

The aphid *Acyrtosiphon calvulus* Ossiannilsson (Homoptera: Aphididae) is one of the world's rarest and most localized insect species. It is currently recorded from just four sites in Sassendalen, Adventdalen, Vestpynten, and Colesbukta, clustered within a 50-km radius on the west coast of Spitsbergen, the largest island in the Svalbard archipelago, Norway (Figure 1) (Ossiannilsson, 1958; Heikinheimo, 1968; Hodkinson et al., 2004; M Hullé, pers. com.). Even within known sites *A. calvulus* is patchily distributed, with populations occurring as small spatially discrete aggregations. Before our recent description of oviparae and males

(Hodkinson et al., 2004), the species was known only from 15 fundatrices and larvae. Winged morphs and viviparae still remain unknown. Ossiannilsson (1958) suggested that *Poa arctica* R. Br. form *vivipara* (Poaceae) might be the host plant, but Heikinheimo (1968) found specimens of *A. calvulus* under stones. Hodkinson et al. (2004) collected material primarily from *Salix polaris* WG (Salicaceae) and *Pedicularis hirsuta* L. (Scrophulariaceae), but a few individuals were taken from *P. arctica* and other grasses.

A major prediction of climate change models is for global warming to occur soonest and to the greatest extent at high latitudes (ACIA, 2005) and endemic Arctic species such as *A. calvulus* appear particularly susceptible to such climatic effects. This response, however, could be positive or negative, with potentially faster development and improved reproduction being offset against loss of synchrony with host-plant phenology, increased pressure from natural

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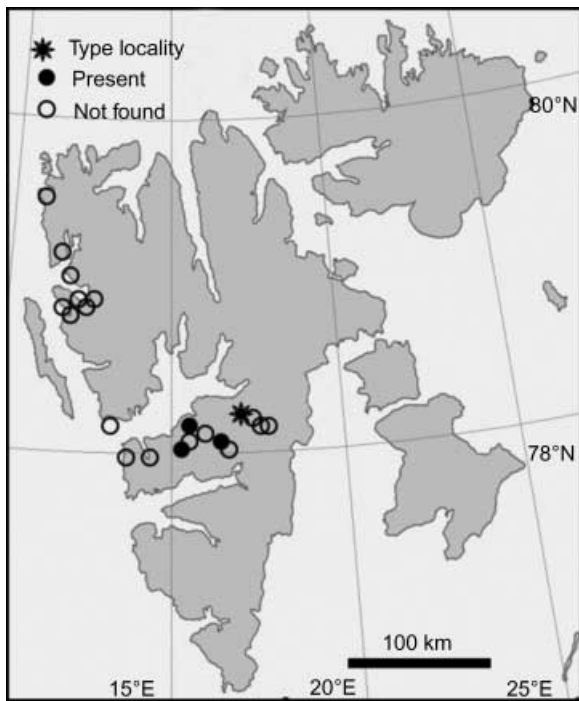


Figure 1 Map of Svalbard, Norway, showing localities from which *Acyrthosiphon calvulus* is recorded (●) and those where it could not be found after extensive searching (○). The type locality is indicated by an asterisk.

enemies, and occasional unsuitably high temperatures. This article therefore aims to examine the abundance, life history, host-plant relationships, and overwintering biology of *A. calvulus* as a precursor to understanding its rarity and potential response to climate change.

The related endemic Svalbard aphid, *Acyrthosiphon svalbardicum* Heikinheimo, monophagous on *Dryas octopetala* L. (Rosaceae), while restricted to warmer sites on the inner fjords of west Spitsbergen (Strathdee & Bale, 1995a), is more common and more widely distributed than *A. calvulus*. *Acyrthosiphon svalbardicum* has a genetically programmed life cycle, overwintering as eggs (Strathdee et al., 1993b, 1995a; Bale, 1999; Hodkinson et al., 2002). Hatching fundatrices produce oviparae and males that mate and lay overwintering eggs. However, they also produce a few viviparae that later, in favourable years, give rise to further sexuales that lay additional eggs. In cooler years there are effectively two generations per year, culminating in overwintering eggs. In warmer years, eggs are still reliably produced from the generation 2 oviparae and males but further eggs are produced by the third generation. Thus, while the fixed basic life cycle contains a genetically predetermined two generations per year, there is also an added element of flexibility that allows response and adjustment to climatic variation.

Another related Arctic species, *Acyrthosiphon brevicorne* Hille Ris Lambers, on *D. octopetala* in Sweden, has a life-history intermediate between *A. svalbardicum* and temperate species in that it has four field generations per year. Fundatrices produce viviparae and sexuales but each succeeding generation gives rise to an increasing proportion of sexuales relative to viviparae, such that by the fourth generation only sexuales are produced (Strathdee & Bale, 1995b; Bale, 1999).

Populations of *A. svalbardicum* and *A. brevicorne* are highly responsive to experimentally raised temperatures, increasing several fold in one season but parasitism and predation later check this initial population increase (Strathdee et al., 1993c; Bale, 1999; Dollery et al., 2006). Above a certain level, enhanced temperature may have detrimental effects on *A. svalbardicum* populations (Dollery et al., 2006). *Acyrthosiphon calvulus* appears similarly responsive to raised ambient temperatures, showing increased abundance in open top chamber warming treatments within a study of the impact of goose grazing on tundra vegetation (FRAGILE project) (Cooper et al., 2004, 2006).

Materials and methods

Study site

The main field studies were conducted on mesic moss heath tundra, with *S. polaris* the dominant vascular plant species, adjacent to the FRAGILE site (78°10'N, 16°07'N) Adventdalen West Spitsbergen, Svalbard, Norway (see Cooper et al., 2006). Additional aphid material was collected at Hotelnesset adjacent to Longyearbyen airport. Laboratory studies were conducted at the University Centre in Svalbard in Longyearbyen and in Liverpool, UK.

A detailed search for *A. calvulus* was made at several sites on fjords along the west coast of Spitsbergen, including Krossfjord and Kongsfjord and around Isfjord during summer of 2005 and 2006, but additional populations were not found, despite known host plants being widespread and abundant (Figure 1).

Host-plant choice and reproduction

Experiments were conducted in 2005 to determine on which host plants *A. calvulus* completed its life cycle. Testing was conducted in field microcosms, each comprising a 5-cm² plastic tub with the bottom and four side window sections cut out and replaced with fine gauze. Each was placed over the target host plant after other species had been clipped and removed. Three plant species were tested: *S. polaris*, *P. hirsuta*, and *Alopecurus borealis* Trinius (Poaceae). Each microcosm initially (30 June) contained five fundatrices with six replicate tubs per plant species. Numbers of aphids per microcosm were counted by direct observation at approximately weekly intervals until 11 August. Two

follow-up tests with *A. borealis* were conducted following the early extinction of the initial population. A sustained increase in aphid population was taken to indicate that *A. calvulus* survived and reproduced on a particular host.

The survival and reproduction of *A. calvulus* on the grasses *A. borealis* (two experiments), *Deschampsia* spec. (two experiments), and *P. arctica* (one experiment) was also tested in the laboratory using individual aphids in Austin tubes (see below). Within each experiment, 8–10 replicates were used, depending on availability. Fundatrices were introduced into the tubes and their survival and numbers of living offspring produced was recorded regularly between 30 June and 8 August.

Life cycle and progeny sequence

Ten newly hatched fundatrix larvae were placed individually on small cut *S. polaris* shoots within culture tubes (Austin et al., 1992) on 5 July 2004, and their survival and progeny output observed over the following weeks (5 July–15 August). Selected female oviparae ($n = 68$) were mated with males and their egg output counted. Tubes were kept outdoors at ambient shade temperature, although shelter from wind resulted in the temperature within the tubes averaging around 1.6 °C higher than the surrounding air over the experimental period. Additional confirmation of the life cycle was obtained from a repeat laboratory study (at ~20 °C) in 2005, using five initial fundatrices over the period 11 July–2 August.

Population studies and host-plant phenology

The phenology of *S. polaris* was observed at regular intervals (weekly or less) throughout 2004 and 2005 on plots in Adventdalen. On each sampling occasion all leaves within 25 stratified random 7.5 × 7.5 cm quadrats were counted and placed into one of five phenological categories: 1, 'bursting' – bud burst but leaves not exposed; 2, 'furled' – leaf not yet unfurled; 3, 'unfurled' – leaf fully expanded/mature; 4, 'senescing' – leaf showing onset of senescence (yellow spotting), and 5, 'senesced' – leaf fully senescent (yellow).

Total aphid numbers were counted by direct observation on the same set of 25 quadrats. To test the efficiency of direct counting in the field, aphid populations were also estimated by taking 30 destructive vegetation samples from within 7.5 × 7.5 cm quadrats on equivalent dates and heat extracting the aphids from the vegetation using Tullgren funnels. Populations estimated by extraction did not differ significantly from those estimated by observation and the former method was subsequently used. Five randomly placed double-sided yellow sticky traps (400 cm²; Agralan, Swindon, UK) were maintained at the site throughout the summer of 2005 to capture dispersing alate aphids.

Thirty-six similar traps were also used adjacent to the main site over 2-day periods in 2003 and 2004 and five 10-cm diameter yellow aphid water traps were maintained on the site during 2005.

Overwintering and hatching of eggs

The supercooling point (SCP) of overwintering eggs was determined, at a cooling rate of 1 °C per min, following Coulson et al. (1995). This involved attaching individual eggs to a thermocouple using a trace of petroleum jelly and cooling within a small enclosed chamber using a Peltier cooling block. The freezing exotherm, seen as a small upward peak in the temperature graph, indicates the release of the latent heat of freezing and corresponds with the SCP temperature.

Overwintering survival was tested in the field using fertilized eggs from laboratory oviparae collected together with the *S. polaris* leaves on which they were laid, with eggs allowed to harden and darken at 5 °C before use. *Salix polaris* leaves, with eggs attached, were glued to the upper surface of 15-cm diameter white plastic discs, with 75 eggs on each of five discs. Discs were placed among *S. polaris* leaf litter in the field 10–100 m apart (sites 1–5) in late August 2004 and left over the winter. The following summer, coincident with snow melt (1 June), discs were examined and numbers of eggs hatching or lost were noted regularly over the following 4 weeks. Two Tinytag® data loggers (Gemini Data Loggers Ltd, Chichester, UK), with the remote thermistor probes placed on the egg disc surface, recorded winter temperature.

Limited laboratory experiments in 2004/2005 showed that *A. calvulus* egg development and hatching occurred under both light and dark conditions at temperatures corresponding to 5 °C or below. A more detailed experiment was conducted in 2005/2006. Eggs collected during late season 2005 were maintained over early winter in the dark at 5 °C. On 16 February 2006, 4 months ahead of the field hatching date, eggs were randomly allocated to four temperature treatments 5, 4, 3, and 2 °C, with 10 eggs per treatment, each replicated five times. Eggs were maintained in the dark but examined weekly in the light until 15 June 2006, when all viable eggs had hatched. They were at no stage exposed to sub-zero temperatures.

Results

Host plants and reproduction

Populations of *A. calvulus* in the field microcosms persisted on *S. polaris* throughout the experimental period, reaching a maximum of eight times their original density (Figure 2). Aphids on *P. hirsuta* showed similar persistence and significantly increased populations, but to a lower maximum

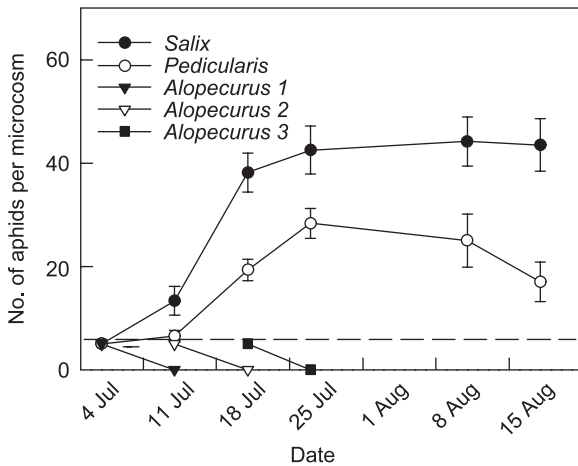


Figure 2 Population densities (\pm SE) of *Acyrthosiphon calvulus* on *Salix polaris*, *Pedicularis hirsuta*, and *Alopecurus borealis* in field microcosm feeding experiments during 2005. Each microcosm initially contained five fundatrices.

($\times 5-6$). Populations on *A. borealis* did not persist and quickly died out without observable reproduction. By contrast with the field results for *S. polaris* and *P. hirsuta*, laboratory survival and reproduction on *A. borealis*, *Deschampsia spec.*, and *P. arctica* was poor (Figure 3). Most fundatrices died within a week, although each averaged between one (*P. arctica*) and three (*A. borealis*) short-lived offspring. Survival to maturity was exceptional. There was nothing to suggest that these laboratory results are not applicable to the field situation.

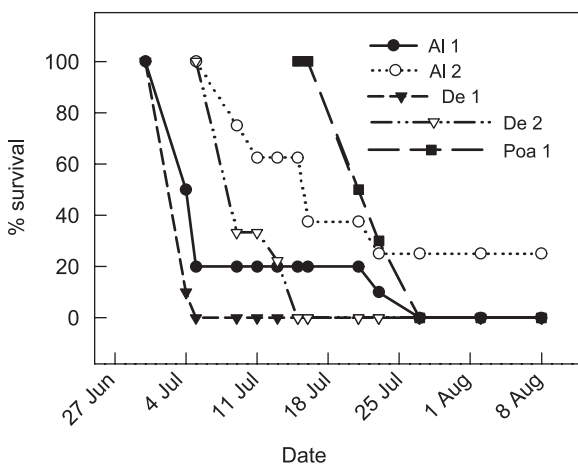


Figure 3 Performance of *Acyrthosiphon calvulus* on *Alopecurus borealis* (Al), *Deschampsia spec.* (De) and *Poa arctica* (Poa) in laboratory feeding trials on grasses during 2005 showing percentage survival of fundatrices over time.

Life cycle and progeny sequence

The life history of *A. calvulus* remained constant in field and laboratory experiments, comprising an overwintering egg that hatched in spring to give an apterous parthenogenetic viviparous female (fundatrix). Each fundatrix produced apterous females (oviparae) and males, following the progeny sequence summarized in Table 1. Males and females then mated to produce the overwintering eggs. Alates were never observed in breeding experiments or field plots and were never caught on the sticky traps or in water traps.

The progeny sequence for field-reared aphids in 2004 was similar to that for laboratory-reared aphids in 2005 (Table 1), with oviparae and males produced approximately equally at first, followed by a long extended tail of oviparae, with only occasional males. This resulted in a strong cumulative female sex bias in the offspring, with male:female ratios of 0.33 ± 0.08 and 0.28 ± 0.04 in 2004 and 2005, respectively. Mean reproductive output (\pm SE) per fundatrix was 29.4 ± 2.75 in 2004 and 24.0 ± 2.89 in 2005. Pre-reproductive mortality among offspring was low ($<8\%$). The reproductive period of the fundatrices extended over 5 weeks, from early July to mid-August, with peak offspring output of in mid- to late-July (Figure 4). Mean number of eggs (\pm SE) laid per ovipara was 9.35 ± 0.72 (range = 1–23).

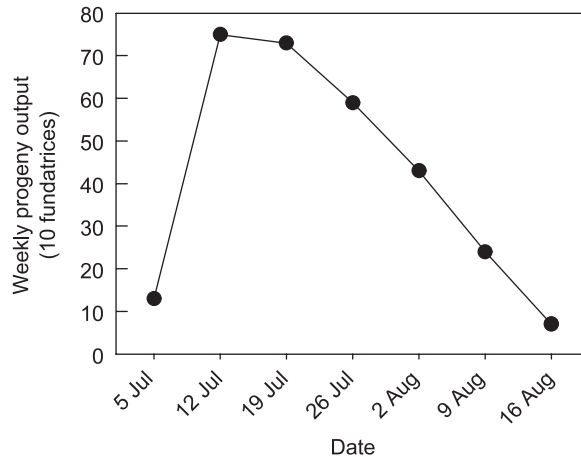


Figure 4 Weekly pattern of progeny output by fundatrices of *Acyrthosiphon calvulus* in the progeny sequence experiments showing the peak in mid-July. Data shown represent the total progeny produced by the 10 experimental fundatrices.

Phenology of *Salix polaris*

Bud burst commenced in both 2004 and 2005 during the first week of June, with most shoots bearing unfurling leaves during the succeeding 2 weeks (Figure 5A,B). Peak numbers of mature, green, fully expanded leaves occurred in mid-July, by which time early senescence was apparent

Table 1 Progeny sequence for fundatrices of *Acyrtosiphon calvulus* maintained on shoots of *Salix polaris* in Austin tube cultures in the field during 2004 and the laboratory during 2005

2004

Tube	Sex	Date										
		5–8 July	9–12 July	13–16 July	17–20 July	21–24 July	25–28 July	29 July–1 August	2–5 August	6–9 August	10–13 August	14–17 August
1	M	2	1	1	1							
	F	4	1	3	5	1	5	5	1	1		
2	M	2	1			1						
	F	4	2		5	2	5	2	2	2		1
3	M	2	3		1							
	F	3			7	6	5	1	1			1
4	M	1	1									
	F		4									
5	M		6			1						
	F	4		2	8	1	6	3	4	1		
6	M	3	3									
	F	2		2	8	1						
7	M		3	2								
	F	2	2		6	3	6	2	2	1	1	
8	M		5			2						
	F	3			5	4	4	3	4	4		
9	M	3	3				1					
	F	3		2	5	1	1	2	5		1	2
10	M		3				1					
	F	4		1	9	1	4	2				2

2005

Tube	Sex	Date						
		8–9 July	10–11 July	12–13 July	14–18 July	19–21 July	22–27 July	28 July–2 August
1	M		2	2				
	F		4		1	3	8	7
2	M		2	2			1	
	F		4		2	1	7	7
3	M		3	1			1	
	F	5			4	1	6	7
4	M			1	3			
	F		2				5	3
5	M		3	1				
	F	1	1		1	1	5	2

in some leaves. Senescence was rapidly advancing by the first week in August.

Aphid population density

The seasonal trend in aphid populations (Figure 5C,D) followed the phenology of the host plant closely. Newly hatched larvae were present on *S. polaris* in early June, as buds began to break. The population increased rapidly until early to mid-July as mature fundatrices began to produce males and oviparae. Beyond this date, the population declined

slowly as mated oviparae commenced laying overwintering eggs, which continued until mid- to late-August. The seasonal decline thus corresponded with the onset of senescence in the *S. polaris* leaves.

Overwintering biology of eggs

Mean (\pm SE) SCP of eggs on entry into the overwintering period in 2004/2005 was -35.3 ± 0.30 °C (range -28.8 to -39.9) (Figure 6). This is below the lowest temperature recorded in exposed snow-free areas during the corresponding winter

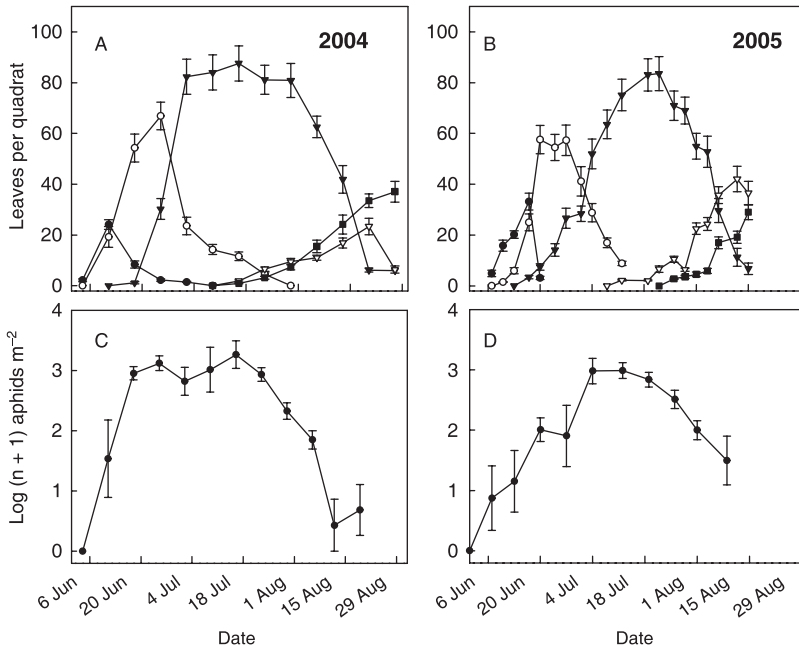


Figure 5 Phenology of *Salix polaris* (A, B) and the corresponding population density of *Acyrthosiphon calvulus* (\pm SE) (C,D) during the summers of 2004 and 2005. Phenological stages are indicated by \blacklozenge - bursting, \blacktriangle - unfurled, \blacktriangledown -senescing, and \blacksquare - senesced.

(-28.4°C). Mean percentage survival (\pm SE) of overwintered egg batches at five locations in the field was 54.1 ± 3.9 . Mortality included ‘winter disappearance’, predation, and attack by fungi. Egg hatch commenced by 8 June 2005, coincident with snowmelt, and was virtually complete by 24 June (Figure 7). Hatching at sites 1 and 2, which were initially flooded, soon caught up with other non-affected sites (Figure 7). Eggs did not require prior exposure to temperatures below 5°C to break diapause and allow development and hatching. Numbers hatching (Figure 8) differed among temperatures (general linear repeated measures analysis of variance using Greenhouse-Geisser correction $F = 20.34$, d.f. = 1.92, $P = 0.001$) and the temperature*time interaction was significant ($F = 10.13$, d.f. = 2.03, $P = 0.006$). Hatch rate at 5°C (60%), because

of high variation among replicates, did not differ from that at 4°C ($P = 0.09$) but hatch at these temperatures was significantly greater than at 3 and 2°C (12 and 10%, respectively) ($P < 0.025$). The rate at $4-5^{\circ}\text{C}$ matched that in field experiments.

Discussion

Experiments demonstrated that *S. polaris* and *P. hirsuta* both serve as host plants for *A. calvulus*. Fundatrices reared

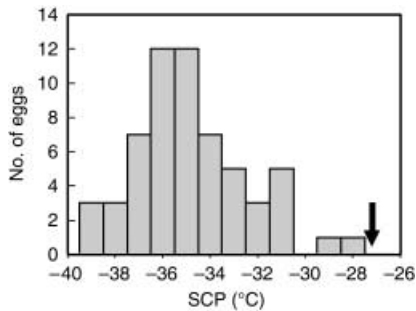


Figure 6 Frequency distribution of supercooling points (SCP) of non-acclimated *Acyrthosiphon calvulus* eggs at the onset of winter 2004/2005. The lowest microhabitat temperature recorded during that winter is indicated by the arrow.

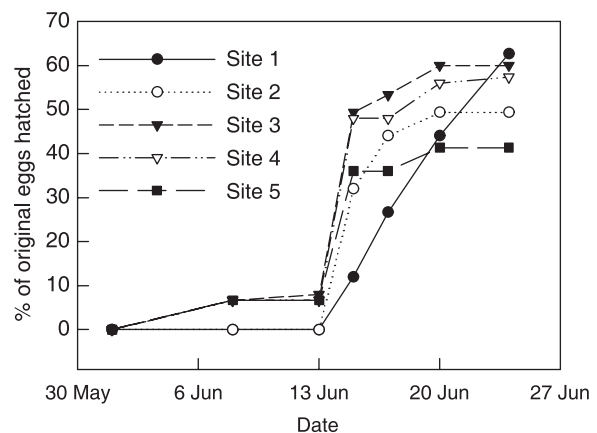


Figure 7 Egg hatching of *Acyrthosiphon calvulus* during early summer 2005. Each line represents the hatching pattern for 75 eggs at each of five locations within the study area. Data are plotted individually to illustrate the variation between site 1 and sites 4-5. See text for further explanation.

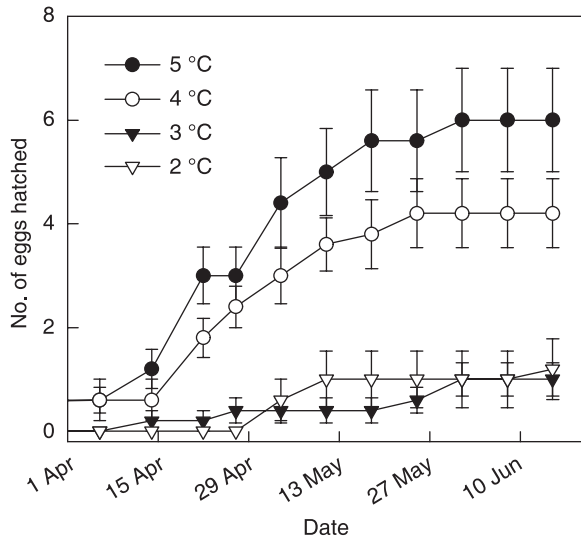


Figure 8 Mean number (\pm SE) of *Acyrthosiphon calvulus* eggs hatching at different temperatures under controlled laboratory conditions.

on *S. polaris*, however, showed high mortality on the grasses *A. borealis*, *Poa*, and *Deschampsia* spec., with few offspring produced and almost none surviving to maturity. This suggests that the limited offspring production on grasses uses residual capital stored during previous growth on *S. polaris*. The host-plant association with *S. polaris* and *Pedicularis* is interesting as *P. hirsuta* is a probable root parasite of *S. polaris* (Freytag & Weber, 1987). The two, however, belong to distantly related families (Scrophulariaceae and Salicaceae, respectively). The use of unrelated hosts by *A. calvulus* may indicate some chemical similarity between the two plant species. *Pedicularis hirsuta*, while common, is scattered as individual plants within a carpet of *S. polaris*. There was no evidence for host alternation by *A. calvulus*.

The holocyclic life cycle of *A. calvulus* is closely synchronized to the phenology of *S. polaris*. For many similar aphids on woody plants, such as *Rhopalosiphum padi* and *Drepanosiphum platanoides*, the midsummer period of leaf maturity represents one of unfavourability when low concentrations of available soluble nitrogen in the leaf restrict aphid growth and reproduction (Dixon, 1970, 1971). This may be why many such aphid species seek alternate summer hosts (Moran, 1992). Aphid performance, by contrast, is maximal during periods of soluble nitrogen mobilisation when leaves are expanding or senescing. The midsummer period of leaf maturity is compressed in *S. polaris*: leaves senesce almost as soon they mature, precluding the need for host alternation by *A. calvulus*. Leaf expansion thus matches the period of reproduction by

fundatrices while the period of senescence corresponds with egg production by mated oviparae.

Host-plant condition may also provide a partial explanation for the patchy distribution of *A. calvulus*. Known populations were all found on well-drained ridges, where *S. polaris* appears under water stress, and were absent from wetter low lying areas where the host plant grows more vigorously. This may relate to enhanced soluble nitrogen levels in stressed plants (Koricheva & Larsson, 1998; Huberty & Denno, 2004) and/or the longer and warmer growing season on the ridges (Hodkinson et al., 1999).

The two-generation life history of *A. calvulus* involving fundatrices and sexuales appears genetically programmed, resembling that of *A. svalbardicum* but lacking the partial third generation of viviparae (Strathdee et al., 1993b). There is consequently no apparent mechanism (viviparae) for enhancing reproductive output during warmer years. Like other Arctic *Acyrthosiphon* species, *A. calvulus* appears to lack the interval timer common in temperate aphids in which a non-predetermined number of generations of summer viviparae provide the driving force for population expansion (Strathdee et al., 1993b). Whether such viviparae (and alates?) are sporadically produced under particular conditions remains open to speculation.

The progeny sequence of fundatrices, in which apterous females and males are produced from the outset, resulted in a strongly female-biased sex ratio of 0.33 and 0.28 in 2004 and 2005, respectively, comparable with values of 0.30 and 0.35 in *A. svalbardicum*. Such biased sex ratios provide evidence for local mate competition within the aphid population. This suggests that selection in *A. calvulus* is favouring the production of the sex (female) that is most likely to provide the highest fitness returns per unit of investment under the prevailing condition of the *S. polaris* host plant and environment (Dagg & Vidal, 2004; Leather et al., 2005).

Based on the measured mean progeny output of 29.4 per fundatrix, a progeny sex ratio of 0.33 and a mean egg output of 9.4 per ovipara, the population of *A. calvulus* is potentially capable of increasing by a factor of 184 in one summer season. This compares with a value of 137 (our calculations) for *A. svalbardicum* during a short cool summer with two generations. It is significantly lower than the 873 progeny *A. svalbardicum* might achieve in a warm year with a partial third generation. *Acyrthosiphon calvulus* may thus be less responsive to the immediate effects of environmental warming than *A. svalbardicum* (Strathdee et al., 1995a; Bale, 1999).

Winter survival of *A. calvulus* eggs was high (>54%), with all eggs having an SCP lower than the minimum recorded winter temperature. Mean SCP of non-acclimated eggs

(−35.3 °C) was comparable with those of *A. svalbardicum* (−36.2 °C) and *A. brevicorne* (−35.5 °C), as were the range of values (−28.8 to −39.9 °C compared with −27 to −43 and −32 to −41 °C, respectively) (Bale et al., 1994; Strathdee et al., 1995b). The effect of extended exposure to low subzero temperatures above the SCP, however, was not tested experimentally and it is not possible to determine whether intact unhatched winter eggs succumbed to cumulative cold or fungal infection.

Egg development and hatching occurred at 5 °C and below, with no apparent requirement for a subzero cold exposure to break diapause and with eggs hatching 3 months ahead of those in the field. Hatch rate at 5 °C (60%) was slightly higher in the laboratory than in the field (51%). Hatching success, however, declined rapidly with decreasing temperature down to 2 °C (12%). Eggs hatched under light and dark treatments, suggesting that larval emergence will take place when eggs are covered by accreted leaf litter, and occurring in response to rising spring temperature immediately following snow melt. Egg development at low temperatures ensures that larvae hatch slightly before or coincident with *S. polaris* bud burst in early summer (Figure 5), allowing them to seek out and colonize the opening shoots as they appear. Water logging during snowmelt may, however, slightly delay hatching at some sites.

The question remains, however, as to why *A. calvulus* is so uncommon and so patchily distributed on a host plant that is common, widely distributed, and frequently the dominant species on Svalbard, often exceeding 50% ground cover (Elven & Elvebakk, 1996). The aphid population is highly fragmented and exists as highly isolated subpopulations within the landscape mosaic. Lack of an alate morph capable of dispersing just short distances, even at high local densities, appear to compound the aphid's difficulty. There is no evidence for wind or water-assisted dispersal by apterous forms, although eggs attached to wind-blown *S. polaris* litter may be dispersed over short distances (Fahnestock et al., 2000). Whatever the dispersal method used, the present distribution suggests that dispersal by *A. calvulus* is, under prevailing conditions, ineffective. This contrasts sharply with many temperate species where local competition usually induces the production of alate colonizing morphs. Wide variation in alate production among clones of temperate *Acyrtosiphon pisum* Harris may, however, provide a clue at how the apparently apterous state could have arisen in an isolated population of *A. calvulus* (Hazell et al., 2005). Existing populations of *A. calvulus* appear too widely dispersed (several km apart) to represent a true metapopulation with source and sink populations as in some other aphids (Massonnet et al., 2002; Martinez et al., 2005; Weisser & Harri, 2005). It is difficult

to envisage how colonies suffering random extinction, perhaps associated with an infrequent extreme climatic event or frost heave, might recover within a reasonable time interval. Despite these limited dispersal abilities, *A. calvulus* appears physiologically well adapted for surviving the Arctic environment. It successfully survives extreme winter low temperatures in the egg stage. Its reproductive capacity, linked to rapid development through two generations within the restricted growing period, even in colder years, suggests that the aphid has the ability to reproduce sufficiently rapidly to maintain a stable or expanding local population under prevailing conditions. It is thus conceivable that the current patchy distribution may represent a relict distribution from earlier warmer times during the early to mid-Holocene (Salvigsen et al., 1992). Warmer future conditions, as predicted by climate change models, may thus lead to increasingly successful reproduction in *A. calvulus* and a rapid rise in the local population, a phenomenon already recorded in open top chambers on Svalbard.

Acknowledgements

We thank the British Ecological Society for a Small Project Grant (MG), the National Science Foundation under agreement no. OPP-0002239, and the National Oceanic and Atmospheric Administration under Agreement no. NA67RJ0147 (IH) for financial support. The article represents a collaborative contribution towards the EU fifth framework project FRAGILE (Fragility of Arctic goose habitat: impact of land use, conservation and elevated temperature, EVK2-2001-00235) in Adventdalen, Svalbard (ISJ). We also thank Jeff Bale for access to his SCP apparatus when ours died and Roger Blackman for identifying our aphid material.

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