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Life-cycle and morph production in the Arctic aphid *Acyrthosiphon brevicorne*

Abstract The life-cycle of the sub-Arctic, *Dryas*-feeding aphid, *Acyrthosiphon brevicorne*, is described and shown to be intermediate between that of the high-Arctic aphid (*Acyrthosiphon svalbardicum*) and typical holocyclic, monoecious, temperate species. The fundatrix of *A. brevicorne* can give rise directly to both sexual morphs, a necessary adaptation to the short Arctic summer. Production of males is predetermined; some males are produced by all-viviparous mothers, but at lower frequencies in the birth sequences of the fundatrix than in subsequent generations. By contrast, the production of oviparae is controlled, at least in part, by photoperiod.

Introduction

The life-cycles of temperate aphids are varied and complex (Lees 1966; Hille Ris Lambers 1966). Some species (e.g. *Myzus ascalonicus* Doncaster) and clones [e.g. *Myzus persicae* Sulzer, *Acyrthosiphon pisum* (Harris), *Rhopalosiphum padi* (L.)] in temperate regions overwinter as active stages (anholocycly) and do not respond to the environmental cues that induce sexual morphs. Active stages usually have a limited capacity to survive cold; thus the ranges of most anholocyclic species and clones are limited by winter temperatures (Knight and Bale 1986; Bale et al. 1988; Parish and Bale 1993; Hutchinson and Bale 1994).

Most species in cold temperate regions have holocyclic clones that overwinter as eggs, which are more resistant to cold than active stages (Way and Banks 1964; Leather 1980, 1981; James and Luff 1982, Strathdee et al. 1995). After a period of diapause, the higher temperatures of spring induce egg hatch producing the fundatrix generation (Behrendt 1963; Way and Banks 1964; James and Luff 1982). From the fundatrix through successive summer generations to autumn the aphids reproduce parthenogenetically and viviparously, with great potential to increase their population size. Overcrowding or poor host quality may initiate the production of winged (alate) morphs that disperse to colonise new plants (Bonnemaison 1951; Lees 1961, 1966; Hille Ris Lambers 1966). Decreasing temperatures and increasing night-length in autumn induce changes in morph type that lead to oviposition (Marcovitch 1923, 1924; Lees 1959, 1966; Hille Ris Lambers 1966; Blackman 1975; Harrington 1984; Ward et al. 1984). In species that remain on the same host plant throughout the year (monoecious), sexuparae are produced that give rise to oviparae and males that mate and lay overwintering eggs (*Aphis chloris* Koch, *Brevicoryne brassicae* L., *Acyrthosiphon pisum*, *Megoura viciae* Buckton) (Wilson 1938; Bonnemaison 1951; Kenten 1955; Lees 1959, 1960). Species that alternate between a summer and a winter host (heteroecious) require two generations before eggs are laid (e.g. *Aphis fabae* Scopoli, *Rhopalosiphum padi*, *Macrosiphum euphorbiae* (Thomas)). Winged males and gynoparae are produced on the summer host and migrate to the winter host where the gynoparae give rise to oviparae. On reaching maturity these mate with the males and lay overwintering eggs (Davidson 1929; Shull 1928, 1942; MacGillivray and Anderson 1964). Although the fundatrix and its immediate successive generations (fundatrigeniae) experience conditions, particularly of photoperiod, that would induce sexual morphs in autumn, this is suppressed by an endogenous mechanism, the interval timer (Marcovitch 1923; Wilson 1938; Lees 1960, 1961).

Notable exceptions to these general life-cycle types have been found in monoecious aphids on woody hosts. These include *Masonaphis maxima* Mason and gall-forming aphids e.g. *Hormaphis hamamelidis* (Fitch) and *Dysaphis devecta* (Walker), which produce sexual

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morphs after two asexual generations in response to poor host-plant quality (Gilbert and Gutierrez 1973; von Dohlen and Gill 1989; Forrest 1970). A further variation occurs in *Eucallipterus tiliae* L., where a low threshold of response to day-length combined with short generation time results in the sexual morphs appearing early in the summer (mid-June); this is an adaptive response to years when the aphid disappears locally before the onset of autumn (Dixon 1972).

The life-cycle of a high-Arctic aphid was first described for *Acyrthosiphon svalbardicum*, a species thought to be endemic to Svalbard (Strathdee et al. 1993a, b). *Acyrthosiphon svalbardicum* has a mono-ecious holocyclic life-cycle on *Dryas octopetala* L., how-ever, it is markedly different from that of temperate species. The production of all morphs is pre-deter-mined and not controlled by environmental cues; the fundatrix gives rise directly to both sexual morphs, a process prevented by the interval timer mechanism in temperate species. Despite having a pre-determined sequence of morphs in its natural environment, the aphid retains flexibility by producing viviparae in the second generation that give rise to another generation of sexuals. This third generation only matures in the most climatically favourable years but then adds mark-edly to the number of overwintering eggs (Strathdee et al. 1993c). Unlike other aphid species, all morphs are apterous, and experimental crowding does not induce the production of alates.

To aid our understanding of the differences between the life-cycles of monoecious, holocyclic aphids in the high Arctic and those from temperate zones, a comparative study was conducted on *Acyrthosiphon brevicorne* HRL (cf *Acyrthosiphon brevicornis*) from the Swedish sub-Arctic, which shares the same host plant, *Dryas octopetala*, as *Acyrthosiphon svalbardicum* (Ossiannilsson 1959; Hille Ris Lambers 1960). A num-ber of questions were addressed: (1) Does *Acyr-thosiphon brevicorne* have an interval timer mechanism? (2) Is the production of sexual morphs photoperiodi-cally cued or genetically pre-determined? (3) Is *Acyr-thosiphon brevicorne* able to produce alate morphs, and if so, in which generations? and (4) How does the life-cycle biology of *Acyrthosiphon brevicorne* compare with those of aphid species from the high Arctic and temperate regions?

Materials and methods

Aphid culturing

On 20 May 1993 field-collected eggs of *Acyrthosiphon brevicorne* from sites close to the Abisko Scientific Research Station in Swedish Lapland were established in culturing tubes (Austin et al. 1992) in environments of different temperature and photoperiod as described in the following sections. These manipulations were designed to determine the factors influencing the production of sexual morphs. Aphids were kept on small excised shoots of *Dryas octopetala*

collected from the field sites and observed at daily intervals. Dates of birth and maturation were recorded, and any new-born progeny were transferred to new culturing tubes or discarded. Shoots of the host plant were replaced at least every 14 days. All experiments were carried out at the Research Station.

Life-cycle in field conditions

The life-cycle in near-natural conditions was determined by follow-ing 15 clones and their progeny throughout the summer until all the viviparae had died or ceased reproduction. Individual fundatrices were reared from egg hatch through to maturity in culturing tubes exposed to field temperatures and light conditions. When fundatri-ces began reproducing, their progeny were removed daily, kept at a level of three individuals in each culturing tube, and reared to adulthood. On maturation, the morph type of these aphids was determined and their position in the birth sequence of the mother was noted. A number of randomly selected nymphs, from the start of the birth sequence of each fundatrix, were reared singly and the progeny sequence of one of these was followed. In turn, their progeny were removed and reared to adulthood under the same conditions. This process was repeated until the end of the season when no more viviparae were produced.

Life-cycle in elevated temperature with natural light

To determine the effect of temperature elevation on the life-cycle of *Acyrthosiphon brevicorne*, 15 eggs were established individually in culturing tubes at approximately 22°C with natural light (on a lab-oratory window sill) on 20 May. Emergent fundatrices were reared to adulthood and a sub-sample (one in three) of their progeny was collected and maintained individually under the same conditions as the mother. On maturation, the morph type of these aphids was recorded and 15 randomly selected viviparae retained. Their progeny sequences were determined in a similar manner. This pro-cess was repeated throughout the summer until no more viviparae were produced.

Effect of short photoperiod on fundatrix and fundatrigeniae birth sequences

To determine whether an interval timer mechanism operates in *Acyrthosiphon brevicorne*, 15 fundatrices were established in field conditions and in the laboratory under photoperiodic manipulation. Between 2130 hours and 0930 hours the cultures were covered with aluminium foil to exclude light. One in three of the progeny was collected, raised to adulthood individually in tubes and the morph type determined. Additionally, 15 randomly selected viviparae pro-duced by the fundatrices in the laboratory in a 12-h photoperiod were kept and their birth sequence followed.

Life-cycle in continuous daylight

A culture was maintained in continuous daylight at 15°C in a growth cabinet to determine whether or not a *Acyrthosiphon brevicorne* would continue to reproduce asexually under these conditions.

Effect of photoperiod manipulations on birth sequences of third generation viviparae

To determine the effect of photoperiod on *Acyrthosiphon brevicorne*, 15 third generation newly born nymphal viviparae, from cultures

reared in elevated temperature (22°C) conditions and natural light, were reared to adulthood in each of 5 photoperiodic (light:dark LD) regimes as follows: 24:0 LD; 20:4 LD; 16:8 LD; 12:12 LD; and 16:8 light (L):shade (S) (shade = 60% of incident light excluded by covering with hessian cloth) (Havström et al. 1993). The L:S cycle was designed to represent the photoperiodic conditions around midsummer, when, although the sun is above the horizon all day there is considerable diel variation in solar angle. Following maturation, the first 25 progeny of these mothers were collected, reared to adulthood in the same conditions as their mother and then their morph type determined.

Production of alatae

Newly hatched fundatrices and newly born second generation viviparae were raised on a small excised shoot of *Dryas octopetala* at one, four and eight aphids per tube at approximately 22°C under natural photoperiod conditions on a windowsill. On maturation, nymphs were removed each day and reared in either of two densities: (1) maintained, keeping the nymphs at the same density of crowding as the mothers, or (2) relaxed, by rearing the nymphs individually in tubes. On reaching adulthood the number of alate morphs was recorded. When mortalities occurred, aphids from different tubes were amalgamated to maintain the same intensity of crowding throughout development.

Performance of alate and apterous viviparae

The time taken to develop to adulthood, the number of nymphs produced each day, the length of reproductive life and the length of adult life were compared for alatae and apterae reared under the same conditions.

Results

Life-cycle

The life-cycle of *Acyrthosiphon brevicorne* under field conditions in 1993 showed that some sexual morphs are produced in all generations following the fundatrix, with the number of oviparae increasing with generation. The final (fourth) generation consisted exclusively of sexual morphs (males and oviparae).

The number of generations per year increased to seven at a mean laboratory temperature of 22°C. Only parthenogenetic females (viviparae) and males were produced by the fundatrix, and the seventh generation consisted exclusively of sexual morphs. The logit-transformed proportion of oviparae in each generation compared to total female production was plotted against the mean date on which the mothers' generation matured to adulthood at both the field and elevated temperatures (Fig. 1). Regression lines plotted through these data showed a strong linear relationship between Julian date and ovipara production expressed as the logit-transformed proportion of female progeny, demonstrating that oviparae production is independent of generation and is determined by some factor dependent on Julian date, probably the photoperiod (elevated
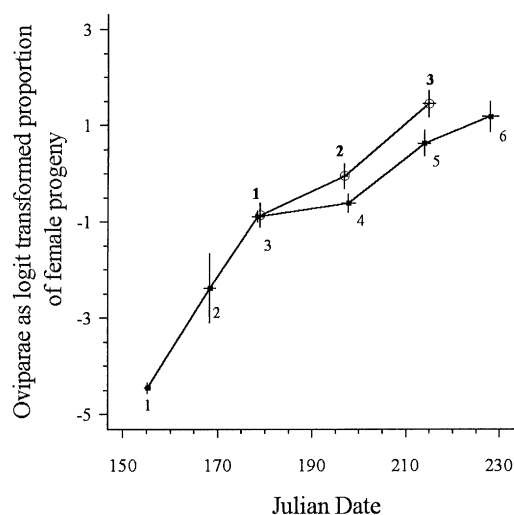

Fig. 1 Production of oviparae as logit-transformed proportion of female progeny of *Acyrthosiphon brevicorne* in field (–○–○–) and laboratory (–■–■–) conditions. *Error bars* are standard errors, *numbers* indicate parent generation of each data point (field in *bold*, laboratory *normal*)

temperature: $r^2 = 0.77, P < 0.001$; field conditions: $r^2 = 0.56, P < 0.001$).

Effect of photoperiod on progeny sequences

In the analysis of the production of oviparae by fundatrices, both photoperiod and temperature produce significant effects (Table 1). The difference between the birth sequences in the laboratory and 'field' conditions may be an effect of the longer development time in the field, which resulted in these aphids experiencing different photoperiodic stimuli. In the laboratory, a short photoperiod increased the production of oviparae in the progeny of the fundatrix and resulted in a third generation consisting entirely of sexuals, but no similar significant increases were observed under field conditions. This suggests that the cues received by the aphids in the field exposure and those in the 12-h photoperiod were equally effective in producing oviparae.

In continuous daylight in incubators at 15°C *Acyrthosiphon brevicorne* completed eight generations in the summer. The proportion of oviparae increased with generation until the eighth generation, which consisted entirely of oviparae and males.

In the experiments manipulating the photoperiod experienced by third generation viviparae, the highest number of oviparae was produced in the regimes that included a period of dark during each day (Table 2, Fig. 2). This finding, together with data on the life-cycle in the field and in an elevated temperature regime, demonstrates that short dark periods (4 h or less) are sufficient to induce the production of oviparae. The most viviparae were produced in the 16:8 light:shade regime. That all groups were not homogenous emphasises

Table 1 Production of oviparae by fundatrices subjected to both temperature and photoperiodic manipulation. Long photoperiod is prevailing natural light, short is with 12-h dark period. Low temperature is field conditions, high is at elevated temperature. *F*-ratios are all based on residual mean square for error

Level		Count n	Average	SE	Source of variation	Sum of squares	df	Mean squares	F-ratio	Significance level ($P =$)
Grand Mean		48	11.53	1.25	Main effects					
A: photo	Long	24	6.96	1.77	A: photo	997.01	1	997.01	13.32	0.0007
	Short	24	16.11	1.77	B: temp	452.31	1	452.31	6.04	0.0180
B: temp	Low	26	14.61	1.69	Interactions					
	High	22	8.45	1.84	AB	718.01	1	718.01	9.59	0.0034
AB	Long out	13	13.92	2.40	Residual	3294.60	44	74.88		
	Long in	11	0.00	2.61	Total (corrected)	5331.92	47			
	Short out	13	15.31	2.40						
	Short in	11	16.91	2.61						

Table 2 Analysis of variance of morphs produced in first 25 progeny by third generation mothers subjected to photoperiodic manipulations. Homogenous groups determined by Tukey's comparison of means (*Levels* **1** = 16:8 L:S, **2** = 24:0 L:D, **3** = 20:4 L:D, **4** = 16:8 L:D, **5** = 12:12 L:D)

Morph: vivipara Source of variation	Sum of squares	df	Mean square	F-ratio	Significance level	Level	Homogenous groups
Between groups	487	4	122	15.7	0.0000	1	x
Within groups	349	45	7.76			2	x
Total (corrected)	836	49				3	xx
						4	x
						5	x

Morph: ovipara Source of variation	Sum of squares	df	Mean square	F-ratio	Significance level	Level	Homogenous groups
Between groups	576	4	144	9.3	0.0000	1	x
Within groups	694	45	15.4			2	xx
Total (corrected)	1270	49				3	x
						4	x
						5	x

Morph: male Source of variation	Sum of squares	df	Mean square	F-ratio	Significance level	Level	Homogenous groups
Between groups	12.4	4	3.10	0.874	0.487	1	x
Within groups	160	45	3.55			2	x
Total (corrected)	172	49				3	x
						4	x
						5	x

the fact that the production of oviparae is not entirely pre-programmed.

Male production

In all generations after the fundatrix, males were present. There was no significant difference in the number of males produced by each manipulation, either in the birth sequences of the fundatrix or the third generation, suggesting that male production is predetermined. There was, however, a significant difference in the number of males produced by fundatrices compared with later generations reared in the laboratory ($F = 3.788$, $P = 0.0054$, Tukey's comparison of means) (Fig. 3).

Production of alatae

Crowding of fundatrices caused the production of alatae in their direct progeny. No level of crowding produced alatae in subsequent generations. The
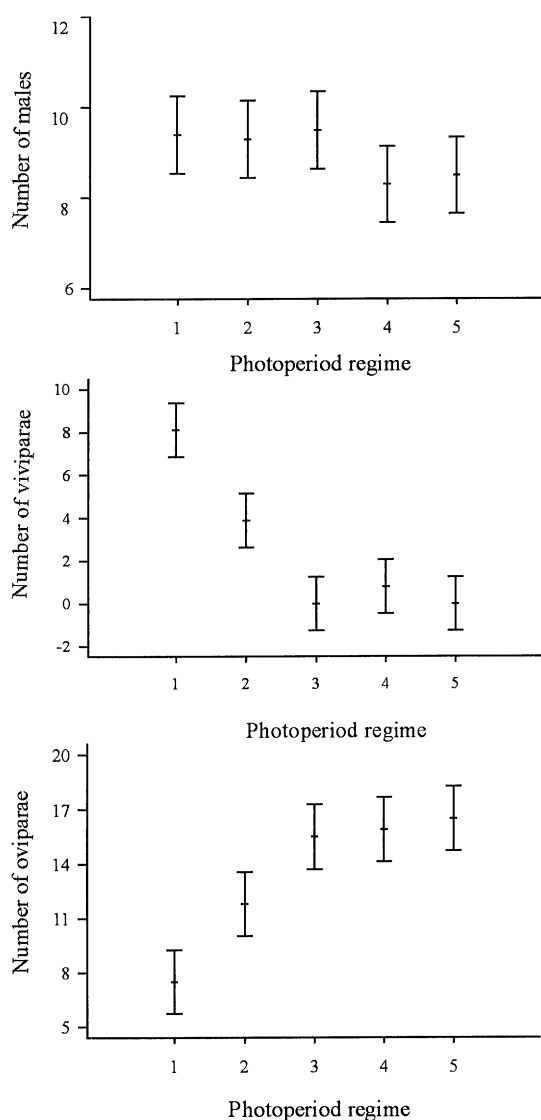
Fig. 2 Production of each morph by third generation mothers at 15°C in five photoperiod regimes (*1*) 16:8 L:S, (*2*) 24:0 L:D, (*3*) 20:4 L:D, (*4*) 16:8 L:D, (*5*) 12:12 L:D. *Error bars* represent standard errors

proportion of offspring maturing as alatae increases with the level of crowding ($\chi^2 = 7.37$, $df = 1$, $P < 0.01$, Fig. 4a). When the crowding pressure is maintained after the birth of the nymphs, a higher proportion develop into alatae than when the crowding pressure is relaxed ($\chi^2 = 26$, $df = 1$, $P < 0.01$, Fig. 4b).

Alatae took significantly longer to develop to adulthood, lived for longer, produced less progeny per day and produced less progeny overall than apterae (Table 3).

Discussion

Male production

In species for which photoperiod induces sexual morphs, long daylength usually prevents production of males as in *Acyrthosiphon pisum* (Kenten 1955), but in some species, such as *Brevicoryne brassicae*, males are produced in long daylength (Bonnemaison 1951). In other species temperature can cue the production of males, independent of photoperiod (*Megoura viciae*) (Lees 1959). Whatever the cue, the production of males by the fundatrix and immediate successive generations of temperate species is restricted by the interval timer. Male production in *Acyrthosiphon brevicorne* is independent of environment and is similar in all generations, except the fundatrix, which gave rise to significantly fewer males in the elevated temperature regime. This lower production of males by the fundatrix suggests a weak interval timer.

Ovipara production

Ovipara production in *Acyrthosiphon brevicorne* was determined mainly by a factor dependent on date: photoperiod plays an important role in this process. The manipulation of photoperiod in the fundatrix and third generation demonstrated that day-length alone induces oviparae, but changes in host-plant quality should not be excluded as a possible further cue. The length of the dark period required to induce oviparae was much shorter than in temperate species, where dark periods of 12 h or more are often necessary to induce sexual females (Lees 1966; Hille Ris Lambers 1966). Austin (1992) found that in field conditions a period of 10 h is sufficient to initiate oviparae in *Rhopalosiphum padi*. In *Acyrthosiphon brevicorne* 4 h of dark in a 24-h cycle induced the exclusive production of oviparae, and shorter dark periods were sufficient to initiate production of at least some. Ovipara production under field and elevated temperature conditions was independent of generation, but was significantly affected by photoperiod and perhaps enhanced by higher temperatures. An experimental approach would determine whether temperature has a real effect. Diurnal variation of temperatures in phase with photoperiodic cues enhances the number of oviparae produced at a particular nightlength in some aphids (Austin 1992). This was not so in *Acyrthosiphon brevicorne* as ovipara production in the more constant elevated temperature regime was higher than that in the fluctuating outdoor regime.

Alate production

Acyrthosiphon brevicorne produces alate morphs in response to crowding, although unlike other members of the Aphidinae, only the direct progeny of the fundatrix can be winged. As with *Acyrthosiphon svalbardicum*, both sexual morphs are apterous. There is a significant cost associated with the growth of flight apparatus by this aphid. The development rate, daily reproduction

Fig. 3a, b Production of males as logit-transformed proportion of total progeny of *Acyrthosiphon brevicorne* in each generation in **a** laboratory and **b** field conditions. *Error bars* are standard errors
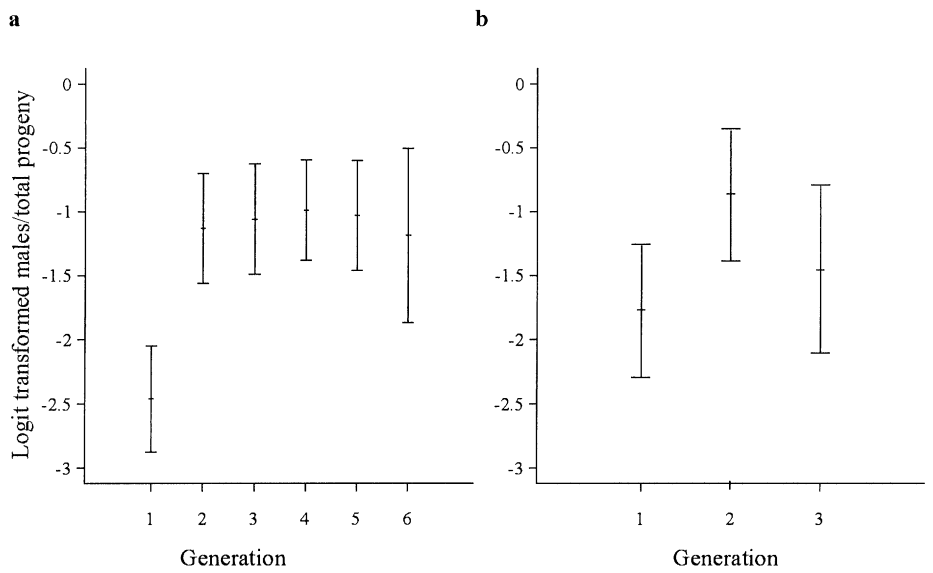

Fig. 4a, b Effect of crowding on the proportion of nymphs maturing as alatae when **a** crowding is maintained after birth and **b** crowding pressure is removed postnatally
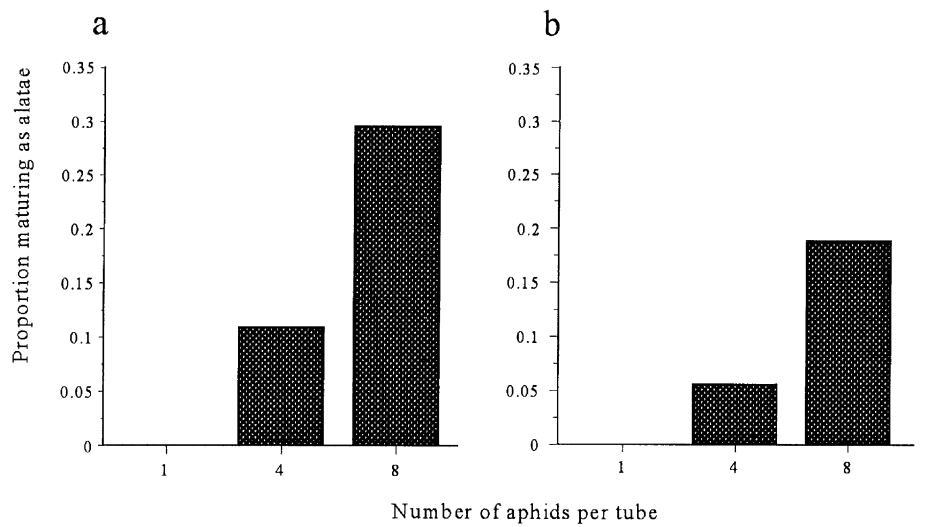

Table 3 Comparative performance of apterae and alatae of second generation viviparae of *Acyrthosiphon brevicorne* (development time, length of reproductive life and longevity are in days)

Measurement	Apterae	Alatae	Significance level
Development time	10.65 ± 0.14	11.75 ± 0.06	$P < 0.005$
Length of reproductive life	18.4 ± 0.22	19.25 ± 2.06	$P = 0.71$
Total longevity	33.9 ± 1.76	40.4 ± 1.7	$P < 0.05$
Progeny per day	1.82 ± 0.08	1.39 ± 0.35	$P < 0.05$
Total progeny	32.2 ± 1.69	23.3 ± 2.27	$P < 0.005$

and the total number of progeny produced are significantly reduced in the alate morph compared to its apterous counterpart, these being the most important factors in the intrinsic rate of increase of an aphid population (Hughes 1963). As with many other species alatae are induced by crowding of the mother but presumptive alatae can also be diverted to become apterae after birth e.g. *Aphis craccivora* Koch (Johnson and Birks 1960; Lees 1966). Wing production relies on crowding of the fundatrix, so alatae would occur only in a year following a favourable season when production of overwintering eggs was high and, moreover, presumptive alatae must also be crowded to maintain a high proportion of winged individuals: conditions would therefore probably have to be favourable in two successive seasons for alatae to be produced.

Interval timer

The birth sequences in many of the temperature and photoperiodic regimes show that the fundatrix of *Acyrthosiphon brevicorne* can produce both sexual morphs directly, a phenomenon only previously recorded in *Acyrthosiphon svalbardicum* among the Aphidinae (Strathdee et al. 1993b). A strong interval timer mechanism is unnecessary in Arctic environments; egg hatch does not occur until mid-summer due to the thermal lag caused by snow melt, and thus there is no risk of premature termination of parthenogenetic reproduction as might occur in temperate species. Indeed, further delay in the production of sexuals would increase the probability that in extreme years Arctic aphids would fail to produce eggs, and become locally extinct. However, the low incidence of males in the progeny of the fundatrix and the increasing numbers of oviparae with generation in continuous daylight suggest a weak interval timer in *Acyrthosiphon brevicorne*. This is clearly not strong enough to prevent the production of sexuals in the progeny of the fundatrix, even under natural conditions. An aphid unable to produce both sexual morphs directly from the fundatrix would have its geographic limit related to a warmer summer isotherm. For example, the thimbleberry aphid (*Masonaphis maxima*) has a distribution determined by the thermal budget (three generations) required for it to maintain existing populations and the extra requirement (two generations) taken to cross gaps of 1 km or more (Gilbert 1982). If the fundatrix gave rise directly to sexual morphs this species would probably be able to persist over a greater range as the thermal requirement required to produce eggs would be reduced.

Truncated life-cycles

Most temperate, holocyclic aphid species have many parthenogenetic generations during the summer, but abbreviated life-cycles have been described for some, particularly in species that are monoecious on their ancestral woody host. For instance, *Dysaphis devecta* has three or four generations, with host plant quality controlling the proportion of sexuals produced. Males are produced throughout the life-cycle and oviparae are produced after three generations, apparently without an interval timer (Hille Ris Lambers 1945; Savzdarg 1955). However, unlike the high-Arctic species, the number of generations is not predetermined and continuous cultures can be maintained without the production of oviparae (Forrest 1970). Similarly *Masonaphis maxima* produces males and oviparae after two parthenogenetic generations but can reproduce asexually for many generations under suitable conditions (Frazer and Forbes 1968; Gilbert and Gutierrez 1973). These life-cycles, although superficially similar to those of Arctic aphids, differ in several respects: firstly, the number of generations is determined by host plant chemistry, whereas in the high Arctic *Acyrthosiphon svalbardicum* the number is predetermined, and in the sub-Arctic *Acyrthosiphon brevicorne* it is controlled predominantly by photoperiod; secondly, the fundatrix does not give rise to a large proportion of oviparae under field conditions; and thirdly, it is not the length of growing season that initiates life-cycle abbreviation in temperate species but poor host plant quality in early summer. Short life-cycles are also known from closely related families (e.g. Pemphigidae) and absence of parthenogenetic forms is found in related superfamilies (e.g. Phylloxeroidea).

Blackman (1974) predicted that the photoperiodic response of holocyclic aphid clones would be adapted to regional conditions. This hypothesis is supported by northern clones of *Dysaphis anthrisci* Börner, *Acyrthosiphon pisum*, *Myzus persicae* and *Rhopalosiphum padi*, which all producing gynoparae and males in response to shorter night lengths (Azaryan 1966; Smith and MacKay 1990; Mittler and Wilhoit 1990; Austin 1992). Here it is shown that this pattern continues with much shorter nightlength cues required in the higher Arctic latitudes; at Abisko (68°N), ovipara production is induced by short nightlength (< 4 h) and on Spitsbergen (79°N) the response to environmental cues is redundant.

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