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ORIGINAL PAPER

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Long life cycle and high adult survival in an arctic population of the mite *Ameronothrus lineatus* (Acari, Oribatida) from Svalbard

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Abstract Field experiments investigated survival and development in an arctic population of the oribatid mite *Ameronothrus lineatus* living on cyanobacterial mats. Mites were sorted to instar and kept in microcosms for 1 year (1997–1998). Juvenile winter survival was high (56–79%), but only about 50% of the adults survived the winter. Summer survival was high in all instars (60–80%). This gave a high survival to adulthood (13.3%). A synchronized moult was observed in July, but juvenile development during the rest of the exceptionally warm summer of 1998 varied both between and within stages, with immatures moulting not at all or up to two times. In a second set of cohorts, experiencing a shorter summer, most juveniles moulted once. Thus, *A. lineatus* has a flexible life cycle with the juvenile stages normally lasting 1 year, giving a larva-to-larva developmental time of 5 years, but with an increased developmental rate in warm summers. Development also seemed to depend on gender, with males developing faster than females. Adult longevity was studied in the laboratory, and most of the adults lived for 2–3 years.

Introduction

Oribatid mites are important members of the soil community in most environments. Several studies have dealt with aspects of the life history of temperate species (Luxton 1981a; Norton 1994). However, studies on life history and demography in cold regions are few, despite oribatid mites being among the few invertebrate taxa that have successfully colonized these environmentally extreme regions (Danks 1981; Marshall and Pugh 1996; Convey 2001). Only the antarctic *Alaskozetes antarcticus* has been studied in detail (Block and Convey 1995). More data on life histories from polar regions of both hemispheres are needed to understand why this group is so successful in cold environments and to elucidate differences between arctic and antarctic species. In particular, what life history traits enable them to survive and develop under the low and characteristically unpredictable summer temperatures?

Developmental rate is the most studied life history trait of oribatid mites, particularly under laboratory conditions, at a single, constant and unnaturally high temperature of 20–25°C (cf. Lebrun 1970; Luxton 1981a). However, the effect of a range of constant temperatures on life cycle length and juvenile development has also been investigated (Lebrun 1974; Weigmann 1975; Bhattacharya et al. 1978; Kaneko 1988; Taberly 1988; Vera and Berthet 1988; Stamou 1989; Enami 1992). While controlled laboratory experiments may uncover causal relationships between variables, results under constant temperature regimes may not be directly transferable to field conditions with fluctuating temperatures. The oribatid mite *Achipteria holomonensis* in the field develops under temperatures much lower than the limit determined in constant laboratory conditions (Stamou 1989). Egg development in *Damaeus onustus* is almost always faster under a fluctuating temperature regime than at an equivalently constant mean temperature (Lebrun 1977).

Thus, laboratory experiments should be complemented with field data to obtain a better understanding of the effect of temperature on development in natural populations. Estimates of developmental time are usually based on the successive appearance of life stages through the field season, with instar peaks allowing cohorts to be followed through ontogeny (Block 1965; Weigmann 1975; Luxton 1981a; Stamou and Sgardelis 1989; Bücking et al. 1998). This technique is useful, but only when oviposition is temporally circumscribed and

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stage-specific developmental times are not too variable. In species with long life cycles and overlapping generations, resulting in stable stage structure and population density (Solhøy 1975; Mitchell 1977; Schatz 1985; Søvik et al. 2003), cohorts may be hard to distinguish and life cycle length and juvenile developmental rates difficult to estimate. Survival may be even harder to estimate from field data since extraction efficiency may vary between life stages (Søvik and Leinaas 2002). Consequently it has rarely been investigated (Norton 1994). These problems can be avoided by using rearing chambers (microcosms) placed directly in the field.

This study focuses on survival and juvenile development in an arctic population of the littoral *Ameronothrus lineatus* in microcosms containing natural substrate. In 1997 and 1998 a field survey on two *A. lineatus* populations inhabiting salt marsh sites on the high arctic Svalbard suggested a long life cycle with juvenile stages developing in approximately 1 year (Søvik et al. 2003). To obtain more detailed data on survival and development from a natural habitat, field experiments using known numbers of stage-determined mites in microcosms were carried out. Each instar, represented by succeeding year classes, was studied through a whole year to obtain developmental and survival rates.

Materials and methods

Field sites

Live material was collected from Colesbukta on West Spitsbergen (78°5′N, 14°57′E). The site consisted of mud flats covered by a 1-mm-thick, smooth layer of cyanobacteria where *Ameronothrus lineatus* was the only arthropod found (Søvik et al. 2003). The virtually two-dimensional substrate is ideal for experiments as all mites were easily observed on the surface and were removed and handled with a soft brush under a stereomicroscope. In contrast to heat extraction, inactive pre-moult quiescent nymphs were also included by this method, and heat induced moulting was avoided. Heat extraction was avoided as it may induce moulting. However, as Colesbukta is remote, field experiments were carried out at a more accessible site. By carefully cutting pieces from the cyanobacteria surface and placing them in microcosms (see below), the cyanobacteria-mite system was transferred to a salt marsh in Adventdalen (78°10′N, 15°30′E), 1 km southeast of the University Centre on Svalbard (UNIS). The salt marsh consisted of wet mud flats covered by *Carex subspathacea* (Arctic salt marsh sedge) and inhabited by a natural population of *A. lineatus*, as well as Collembola and Diptera larvae (Søvik et al. 2003). This natural population, however, could not be studied in situ as the mites were hidden in the *Carex* vegetation.

Species characteristics

A. lineatus follows the general life cycle of an oribatid mite with five active instars: larva, protonymph, deutonymph, tritonymph and adult. Before ecdysis to the next instar, juveniles go through a quiescent stage, becoming turgid and motionless. Hexapod larvae are easily distinguished from the octopod nymphs, while adults are morphologically different from juveniles (Schubart 1975). Stage determination of nymphs requires clearing in lactic acid and counting the number of genital papillae/setae. Our experiments required determination of live nymphs, which was done by sorting by size into three groups: small, medium and large. Overlapping size ranges (Søvik et al. 2003) implied some risk of inaccurate stage determination. To estimate the accuracy, nymphs ($n = 864$) sampled in summer 1998 were sorted to stage based on size, cleared and correctly determined.

Field experiments

Stage-specific winter survival was studied from 1997 to 1998. Mites, sampled on 29 June 1997 and thereafter stored in a cold-storage chamber (2°C), were sorted to instar in September. These ''autumn 97 cohorts'' (A97) were placed on the cyanobacteria layer in microcosms half filled with mud. Microcosms comprised round plastic boxes (height 4.7 cm, diameter 4.2 cm) with plankton mesh for ventilation and drainage. Owing to the low numbers of specimens in the smaller juvenile instars in the 29 June material, the number per microcosm and the number of microcosms varied with stage (Table 1). The larval microcosms were placed out on the tundra, half buried with the inside sediment surface flush with the surrounding ground. An unexpected freezing of the ground resulted in the other microcosms being placed in soil in a plastic tray outside the UNIS building where winter snow cover was thinner than at the tundra site.

Microcosms were checked on 1 July 1998 and winter survival was estimated to this date. Studies of survival and juvenile development were continued throughout summer 1998. Old cyanobacteria were replaced with fresh material before surviving mites were returned to their microcosms. All boxes were then moved to Adventdalen and left for the summer (Table 1). On observation days, microcosms were returned to the laboratory and living mites and

Table 1 Number of microcosms and mites per microcosm for each cohort in the field studies on survival and development, and dates for start of the experiments and counting of the mites

Stage	Microcosms	Mites	1997 Start	1998			
				Counted	Start	Counted	Counted
A97 cohorts							
Larvae	8	16	17 September	1 July			10 September
Protonymphs	6	8	25 September	1 July			15 September
Deutonymphs	8	16	25 September	1 July			15 September
Tritonymphs	8	30	30 September	1 July			22 September
Adults	10	30	23 September	1 July			22 September
S98 cohorts							
Larvae	6	20			16 July	31 July	15 September
Protonymphs	6	20			16 July	31 July	15 September
Deutonymphs	6	20			16 July	31 July	15 September
Tritonymphs	6	20			16 July	31 July	7 October
Adults	6	20			16 July	31 July	30 September

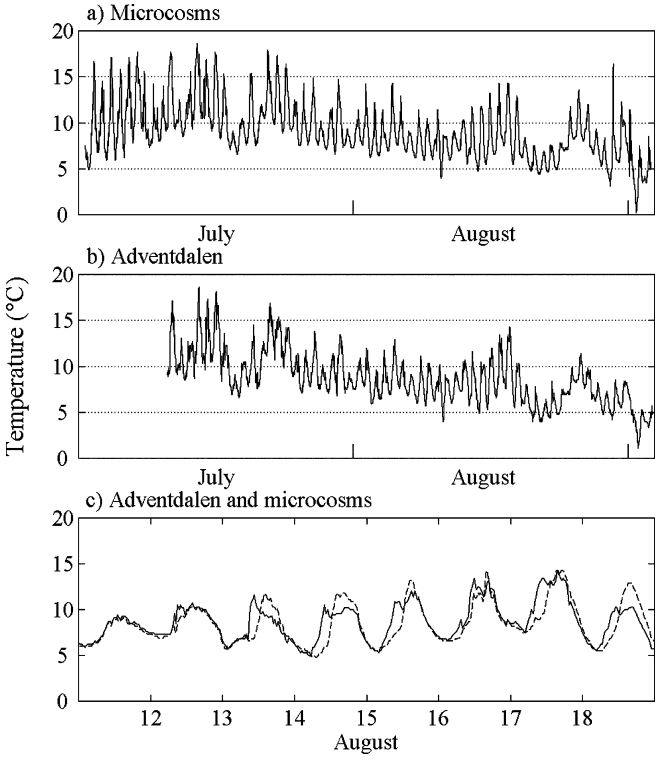

Fig. 1a–c Soil surface temperature recordings (°C), summer 1998. **a** From a microcosm (1 July–3 September, every 15 min). **b** From the Adventdalen study site (11 July–3 September, every 30 min). **c** Recordings from the Adventdalen study site and the microcosm combined for comparison of daily temperature fluctuations (11–18 August); note different scales on *x*-axes. *Solid line* (—) Adventdalen recording, *dashed line* (—) microcosm recording

quiescent juveniles counted. To prevent living juveniles being removed, all immobile juveniles were assumed to be quiescent. Immobile adults were considered dead and were removed.

To address the risk of overlooking some individuals during observations, we placed 6×20 mites of each stage, collected on 23 June 1998, into microcosms as described above. These "summer 98 mites" (S98) were placed at Adventdalen on 16 July 1998. Fifteen days later, when probably little or no mortality had occurred, mites were counted and retrieval rates calculated. To obtain additional information on survival and development, the S98 mites were returned to the field site and left for the rest of the summer (Table 1). Three weeks in the cold-storage chamber meant that the S98 mites experienced a shorter summer compared with the A97 cohorts. All microcosms were collected on 29 August and the mites counted. Tritonymphs and adults were kept for laboratory experiments. Other juveniles were cleared and determined.

The first part of winter 1997–1998 was unusually mild, while January and February were cold, with mean air temperatures between −20 and −30°C on 18 and 17 days, respectively. Summer 1998 was warmer and drier than normal (data from Norwegian Meteorological Institute). Surface soil temperatures were recorded during summer 1998 with one Tinytalk datalogger [Gemini Data Loggers (UK)] in the Adventdalen site and one within a microcosm (Fig. 1). The average soil temperature (with temperature range) for 11–31 July was 10.8 (6.6–18.6)°C both inside and outside the microcosm. In August the averages were 7.8 (4.0–14.3)°C and 8.0 (3.1–16.4)°C in the control site and microcosm respectively. The cumulative day degree total above 0°C (11 July–3 September) was similar inside (487) and outside (478) the microcosm, as was the daily variation in temperature (Fig. 1c). The microcosms thus closely reflected the thermal environment in the surrounding area.

Laboratory experiments

Laboratory experiments were carried out at the University of Oslo from 1998 to 2001. As it was not feasible to study the mites for several years in the field, adult longevity was studied in the laboratory, where the A97 and S98 microcosms were monitored until all adults had died. One replicate S98 box was accidentally destroyed. In October 1998 surviving adults were gradually cooled and stored at −3 to −9°C in darkness for 4 months, to simulate winter. Preliminary experiments had shown that this was sufficient to obtain "wintering effects" including synchronized moulting and larviposition (Søvik et al. 2003). The length of the "summer" (constant 10°C and 24 h photoperiod) was 3 months, reflecting the length of a typical Svalbard summer (Coulson et al. 1995). At the start of winters and summers, animals were cooled/thawed over 1–2 weeks at decreasing/increasing temperatures (0, 2°C). In this way we intended to simulate three Svalbard "years" in 21 months. However, owing to unforeseen circumstances the second winter (W_2) became 12 months long. This is not much longer than a normal arctic winter (9–10 months) and the experiment was continued. During summer the boxes were kept at 100% humidity and aired once a week. Living adults were counted at the beginning and end of each laboratory summer.

To understand patterns of mortality within the adult stage, we compared survival during the first winter in the laboratory (W_1) of the A97 adults (adults more than 1 year old) with the adults moulting from the A97 tritonymphs during summer 1998 (adults less than 1 year old). A new cohort of tritonymphs collected in Colesbukta on 26 August 1998 was included as a reference. The ten A97 adult microcosms contained 7–23 adults ($n = 120$). Six of the A97 tritonymphal boxes were used, each containing 12–22 newly moulted adults ($n = 108$). The Colesbukta tritonymphs were placed in six microcosms as described above, each with 20 nymphs.

Life-table analysis

A life-table was constructed for the A97 juvenile survival data, differentiating between summer and winter survival. Survival rates were corrected using retrieval rates as described below. Adult survival data were not used, as the age of the adults was unknown. The following parameters were calculated: l_x = number of surviving individuals at the start of stage x, expressed per 1,000 individuals; d_x = number of individuals dying during stage x; $q_x = d_x/l_x$, stage-specific mortality rate; $k_x = \ln(l_x/l_{x+1})$, killing power.

Statistics

Statistical analyses were carried out using S-Plus 2000. Logistic regression models tested for differences between instars in survival, retrieval rate from microcosms and proportion of quiescent specimens on 1 and 31 July. If the residual variance of a model did not fit a binomial distribution (goodness-of-fit test), i.e., if data were overdispersed, the model was refitted using the quasi-likelihood method [link = logit, variance proportional to $\mu(1\text{-}\mu)$]. Original and re-fitted models used the deviance and F-statistic as test statistics respectively. Winter survival rates of the different cohorts were corrected by dividing the proportion surviving (of the pooled samples) by the respective stage-specific retrieval rates, while summer survival rates were corrected using the retrieval rates for the succeeding stage, due to ecdysis during summer 1998. Testing for differences between corrected juvenile survival rates was done using a four-sample, two-sided test for equality of proportions.

Simple linear regression was used to test for a relationship between killing power (k_x) and age. Stage was transformed to age by assuming that juveniles use 1 year per life stage and moult in early summer (Søvik et al. 2003).

It was not possible to test for between-cohort differences in the proportion of juveniles not moulting during summer 1998 owing to a small number of non-moulting individuals. A log-linear model

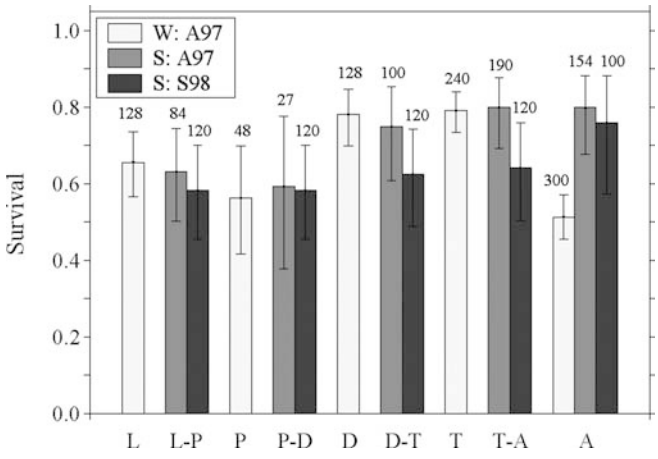

Fig. 2 Cohort-specific winter and summer survival in the field for the A97 and S98 mites (proportions of pooled samples with 95% confidence interval). Winter survival was estimated from September 1997 to 1 July 1998 (*A97*), while summer survival was estimated from 1 July to 29 August 1998 (*A97*) and from 16 July to 29 August 1998 (*S98*). Sample sizes (*n*), given by *figures*, are total numbers of each cohort at the start of the season. The *last three columns* represent survival of adults of mixed ages. *L* Larvae, *P* protonymphs, *D* deutonymphs, *T* tritonymphs, *A* adults

(contingency table analysis) tested for dependency between instar and number of moults in the larvae, protonymphs and deutonymphs. Non-moulting juveniles were pooled with juveniles that moulted once. Thus, the predictor variable "moults" was given two categories, 2 or <2.

Results

Winter and summer survival in the field

Winter survival was high for all instars (Fig. 2), but there was a highly significant difference between stages (logistic regression: deviance = 58.44, $df = 4$, $P < 0.001$), with lowest survival for adults (mixed ages) and highest for deutonymphs and tritonymphs. The difference also remained significant when the data were analysed without adults (logistic regression: deviance = 16.08, $df = 3$, $P = 0.001$). However, as the retrieval rates of the life cycle stages differed significantly with ontogeny, being smallest for larvae and highest for adults (Table 2) (logistic regression: deviance = 46.96, $df = 4$, $P < 0.001$), the survival data were biased. Corrected survival rates (Table 3) resulted in an increased larval rate, which became quite similar to the deutonymphal and tritonymphal rates. However, there was also a significant difference between the corrected juvenile survival rates ($\chi^2 = 9.01$, $df = 3$, $P = 0.03$).

Table 2 Retrieval rates of the five S98 cohorts (with 95% confidence interval). The mites were sorted and placed in the field on 16 July and recounted on 31 July 1998

Stage	Rate	95% confidence interval	n^a
Larvae	0.775	(0.687, 0.844)	120
Protonymphs	0.817	(0.733, 0.879)	120
Deutonymphs	0.892	(0.818, 0.938)	120
Tritonymphs	0.975	(0.921, 0.992)	120
Adults	0.983	(0.932, 0.996)	120

[a]Sample sizes (*n*) denote total number of each stage on 16 July 1998

As most juveniles moulted at least once during summer 1998 (see below), summer estimates refer to survival during the last part of the cohort stages and the first part of the succeeding stages. All A97 cohorts had a high summer survival (Fig. 2), with no significant difference between stages (logistic regression: $F_{4,35} = 1.92$, $P = 0.13$). Adult survival (mixed ages) was higher during summer than winter. Again, corrected summer survival rates resulted in an increased larval rate (Table 3). There was no significant difference in summer survival between the different S98 cohorts (logistic regression: $F_{4,24} = 1.27$, $P = 0.31$). Even though the accuracy of size based sorting of nymphs was dependent on ontogeny (Table 4), this had minor implications for estimated survival rates since juvenile survival did not differ between stages (except a lower survival of the protonymphal cohort).

There was no significant relationship between age and k_x values (linear regression: $F_{1,6} = 0.19$, $P = 0.68$), showing that mortality was independent of juvenile stage. Out of a standardized cohort of 1,000 larvae, 164 survived the tritonymphal stage, while 133 also survived the first summer as adult (Table 6).

Adult winter survival and longevity in the laboratory

Winter survival of the A97 adults (mixed ages) in the field was low compared with survival of the same cohort the following winter in the laboratory (W_1) (Table 5). Survival during W_1 was high also in the newly moulted adults and tritonymphs. There was no difference in laboratory winter survival between the three cohorts (logistic regression: deviance = 1.24, $df = 2$, $P = 0.54$).

Table 3 Corrected winter and summer survival rates (with 95% confidence interval) for the A97 cohorts

Stage	Winter			Summer		
	Survival	95% confidence interval	n^a	Survival	95% confidence interval	n^b
Larvae	0.847	(0.771, 0.904)	128	0.772	(0.667, 0.860)	84
Protonymphs	0.688	(0.532, 0.815)	48	0.664	(0.457, 0.836)	27
Deutonymphs	0.876	(0.802, 0.929)	128	0.769	(0.666, 0.849)	100
Tritonymphs	0.812	(0.754, 0.856)	240	0.814	(0.750, 0.864)	190
Adults	0.522	(0.459, 0.575)	300	0.813	(0.740, 0.875)	154

[a]Pooled sample size at the beginning of the winter season
[b]Pooled sample size at the beginning of the summer season

Table 4 Accuracy of size-based sorting of the nymphal stages

Stage based on size sorting	n[a]	Correctly determined[b]	Stage below[c]	Stage above[d]	Not determinable[e]
Protonymphs	232	0.713	–	0.229	0.058
Deutonymphs	279	0.796	0.011	0.143	0.050
Tritonymphs	353	0.913	0.035	–	0.052

[a]Number of nymphs sorted by size to proto-, deuto- and tritonymphs
[b]Proportion of correctly size-determined nymphs
[c]Proportion of incorrectly size-determined nymphs belonging to the stage below
[d]Proportion of incorrectly size-determined nymphs belonging to the stage above
[e]Proportion of undetermined nymphs (too folded or dirty)

Table 5 Winter survival (with 95% confidence interval) during the first winter in the laboratory for the A97 adults (> 1 year old), adults recently gone through ecdysis (< 1 year old) and tritonymphs. Winter survival for the A97 adults in the field 1997–1998 is included for comparison

	Stage	Survival	95% confidence interval	n[a]
Laboratory	A97 adults	0.917	(0.846, 0.956)	120
	Young adults	0.944	(0.876, 0.976)	108
	Tritonymphs	0.950	(0.888, 0.979)	120
Field	A97 adults	0.513	(0.455, 0.572)	300

[a]Sample sizes (n) denote total number of each cohort at the beginning of the winter

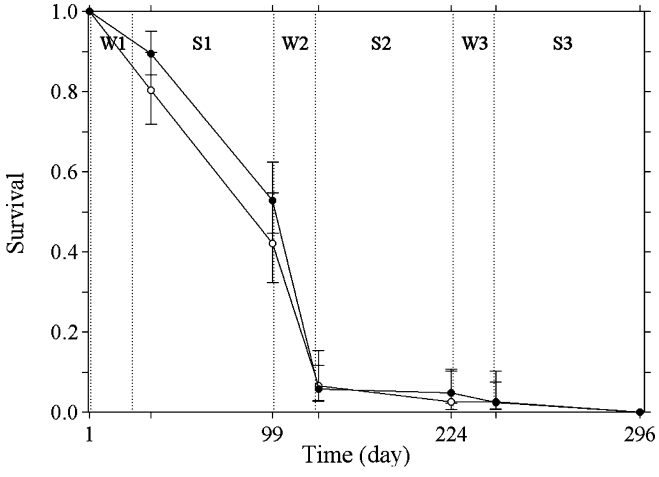

Fig. 3 Survival of the A97 and S98 adults through three experimental years in the laboratory, given as the proportion of the original cohorts surviving (with 95% confidence interval) ($n = 120$ and 76 for the A97 and S98 adults respectively). The winters (*W1*, *W2*, *W3*), which were of unequal length (see text), have been given a standard length to make the figure clearer. Laboratory summers (*S1*, *S2*, *S3*) include only days with temperature = 10°C. *Time* (days after start of experiment) includes only summer days, excluding cooling/thawing periods and winters

The survival curves of the A97 and S98 adults were strikingly similar (Fig. 3). Approximately half of the adults died by the end of the first laboratory summer (S_1) and most were dead after W_2. Most adults (59.2 and 55.3% of the A97, and S98 adults respectively) died during winter. Five females survived three laboratory years. Since the A97 mites were collected before the synchronous moult in July (Søvik et al. 2003) and stored in a cold-storage chamber (where development is slow) until September, it seems likely that little moulting took place during summer 1997. Thus, the A97 adults probably moulted at the latest in summer 1996, implying at least two summers spent as adults in the field. Similar reasoning applies to the S98 adults. Thus, the longest-lived females survived almost five summers.

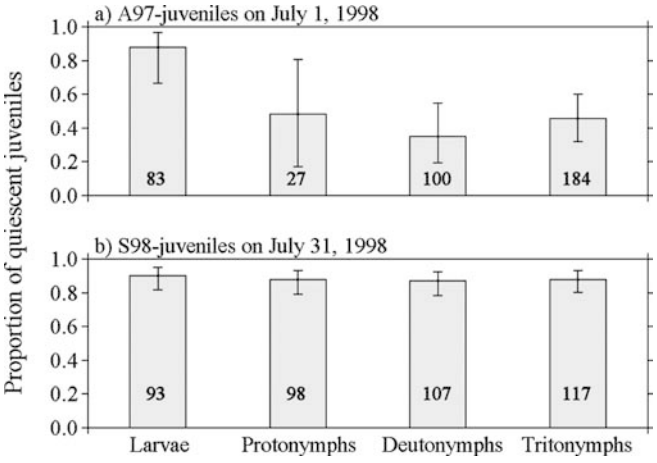

Fig. 4a, b Proportions of pooled samples (with 95% confidence interval) of the different juvenile cohorts in the pre-moult quiescent stage. **a** In the A97 population on 1 July. **b** In the S98 population on 31 July. Sample sizes (n) are given by *figures*

Juvenile moulting and development

Quiescent juveniles were observed in the A97 microcosms on 1 July in varying proportions (Fig. 4a), with differences between cohorts (logistic regression: $F_{3,26} = 5.84$, $P = 0.003$). In the larval microcosms 66.7–100.0% were quiescent and three larvae had moulted to protonymphs. The proportions of quiescent nymphs were lower, and 15 exuviae indicated some moulting. The proportion of quiescent juveniles was variable within stages. Active mites in tritonymphal boxes were still nymphs, except for one with six newly moulted adults. In one protonymphal and one deutonymphal box all juveniles were quiescent, whereas in another deutonymphal box all were active. By contrast, on 31 July a highly synchronized quiescence was observed in the S98 microcosms (Fig. 4b), with no difference between stages (logistic regression: deviance = 0.61, $df = 3$, $P = 0.89$). Three larvae had moulted and three exuviae were found in the nymphal boxes. No adults were observed. Approximately half of the quiescent juveniles (46.4%) were found in clusters of 2–4 specimens (42 clusters) or larger aggregations of 5–7 (5) and 8–10 mites (4).

The precise stage determination in autumn 1998 of the A97 cohorts revealed that juvenile development

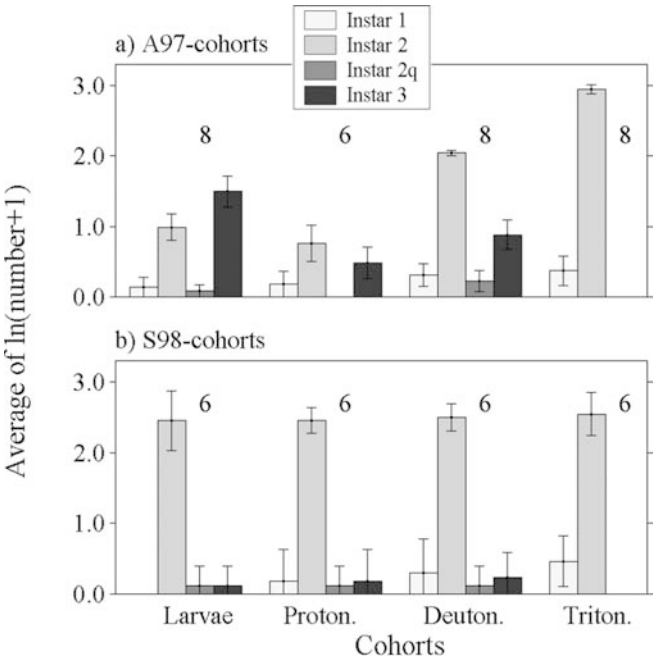

Fig. 5a, b Distribution of instars in autumn 1998, illustrating development through the summer, given as the mean of the natural logarithm (ln) (±SE). **a** In the juvenile A97 cohort. **b** In the juvenile S98 cohort. Sample sizes (*n*), i.e., the number of microcosms, are given by *figures*. *Instar 1* is the initial life stage of each cohort, while *instar 2* and *instar 3* are the two following ones. *Instar 2q* denotes quiescent mites in *instar 2*

varied within as well as between instars. A few juveniles had not moulted during the summer (Fig. 5a). Proportions of non-moulting specimens from pooled cohorts were similar [0.038, 0.125, 0.053 and 0.039, $n = 53$, 16, 75 and 152 (larval-tritonymphal cohorts)]. In contrast, number of moults during summer 1998 depended on stage, as evidenced by a significant interaction in the contingency table analysis (log-linear model: stage*moults, deviance = 28.23, $df = 2$, $P < 0.001$). More larvae and fewer deutonymphs moulted twice than would have been expected with no interaction. Thus, the rate of juvenile development decreased with ontogeny. Developmental rate also seemed to depend on gender, as 10 out of 14 deutonymphs moulting into adults were males. As opposed to the A97 cohorts, development of the S98 juveniles was more synchronous (Fig. 5b). In late August the majority of all stages had moulted once [0.971, 0.929, 0.919 and 0.948, $n = 70$, 70, 74 and 77 (larval-tritonymphal cohorts)].

Discussion

Survival

The habitats of *Ameronothrus lineatus* sampled were characterized by few or no interspecific competitor or predator species (Søvik et al. 2003) and a seemingly abundant food supply suggesting a lack of biotic regulation of the population. Desiccation or extreme summer temperatures probably rarely occur in these habitats, which remain wet and thus thermally buffered, even during the unusually warm and dry summer of 1998 (Søvik et al. 2003). Furthermore, the small difference between summer and winter juvenile mortality, despite the unusually cold January and February of 1998, suggests that low temperature was not a major constraint. Thus, paradoxically, neither biotic nor abiotic factors appear important in the regulation of the population density. However, density-dependent intraspecific effects may regulate the population, especially in high-density patches (Søvik et al. 2003). An effect of prolonged exposure to low sub-zero temperatures is also suggested by comparing winter survival of tritonymphs in the field and laboratory (0.792 vs 0.950).

High survival of deutonymphs and tritonymphs independent of season (with lower survival of protonymphs) is also characteristic of the antarctic *Alaskozetes antarcticus* (Convey 1994). In contrast, juvenile mortality in the alpine *Oromurcia sudetica* decreased exponentially with ontogeny, with 9.5% of the eggs surviving to adulthood (Schatz 1983). This figure is comparable with the estimated 13.3% survival to adulthood in *Ameronothrus lineatus* (Table 6), which excludes the summer mortality of newly deposited larvae. However, an increasing number of larvae in field samples throughout summer 1998 (Søvik et al. 2003) suggests that larval summer survival was high. In both species females overwinter before ovipositon/larviposition (Schatz 1985; Søvik and Leinaas, submitted), suggesting that overall survival to maturity is lower. Laboratory results (Table 5), however, suggest a high W_1 survival of adults, comparable with tritonymphs. High survival to maturation is consistent with a low lifetime reproductive output of ca 20 larvae (Søvik and Leinaas, submitted).

A higher juvenile winter survival probably results from higher juvenile cold tolerance, with oribatid eggs and juveniles having lower supercooling points than corresponding adults (Young and Block 1980; Shimada et al. 1992; Webb and Block 1993; Sugawara et al. 1995; Hansen 2000). Convey (1994) similarly observed that adult survival was slightly lower than nymphal survival in *Alaskozetes antarcticus*. However, mites may experience considerable mortality at temperatures higher than the estimated supercooling points (Convey and Worland 2000) and this might explain why adult mortality in *Ameronothrus lineatus* was higher during the relatively mild laboratory winters than during the summers (Fig. 3; Søvik and Leinaas, submitted). An opposite pattern was observed in *O. sudetica*, where adult mortality rate was higher during summer than winter (Schatz 1983).

High adult longevity, where the majority lived for 2–3 years, is consistent with field data (Søvik et al. 2003) and shows that survival is high for young adults. The relatively low field winter survival of 51.3% (mixed ages) is thus probably not representative of adults aged

Table 6 A97 juvenile survival data for winter 1997–1998 and summer 1998 and calculation of life-table parameters

Stage	Season	Data			Life table			
		n[c]	x[d]	c[e]	l_x[f]	d_x[g]	q_x[h]	k_x[i]
Larvae	W[a]	128	84	108.4	1000.0	153.2	0.153	0.166
Larvae-protonymph	S[b]	84	53	64.9	846.8	192.8	0.228	0.258
Protonymph	W[a]	48	27	33.1	654.0	203.7	0.312	0.373
Protonymph-deutonymph	S[b]	27	16	17.9	450.2	151.1	0.336	0.409
Deutonymph	W[a]	128	100	112.1	299.1	37.1	0.124	0.133
Deutonymph-tritonymph	S[b]	100	75	76.9	262.0	60.5	0.231	0.262
Tritonymph	W[a]	240	190	194.9	201.5	37.9	0.188	0.208
Tritonymph-adults	S[b]	190	152	154.6	163.6	30.5	0.186	0.206
Adults					133.2	133.2	1.000	

[a]Winter 1997–1998
[b]Summer 1998
[c]Total number at start of each season; as cyanobacteria pieces were renewed at start of summer 1998, implying that unobserved specimens in tiny crevices might have been thrown away, the observed number of specimens was used as starting number for the summer season, not the corrected number
[d]Observed number surviving
[e]Corrected number surviving, i.e., x/r, where r = stage specific retrieval rate (Table 2)
[f]Number of surviving individuals at the start of stage x
[g]Number of individuals dying during stage x
[h]Stage-specific mortality rate (d_x/l_x)
[i]Killing power ($\ln(l_x/l_{x+1})$)

1–2 years. However, we did not observe an age-dependent survival when comparing old and young adults during W_1. An adult life span of 2–3 years has also been observed in an alpine and an antarctic oribatid species (Schatz 1985; Convey 1994). In temperate soils, adult longevities of 1–2 years may not be uncommon (Norton 1994).

Juvenile development

The presence of more than 90% quiescent S98 juveniles in late July suggests that moulting was highly synchronized. This represented the first moult following winter as no moulting occurred in the Colesbukta population before the sampling of these mites (Søvik et al. 2003) and as development was probably arrested in the cold-storage chamber. A synchronous early summer moult was also observed in the field in 1998 (Søvik et al. 2003) and has been reported in *Alaskozetes antarcticus* (Convey 1994) and a sub-alpine population of *Trhypochthoniellus setosus* (Kuriki 1995). The less synchronized early summer quiescence in the A97 juveniles could be due to differences in microhabitat temperature in June following melting of the snow. Temperature was probably higher on the tundra site than outside the UNIS building owing to an effect of shading, which explains the apparently faster development of the larvae.

The early summer moult may be synchronized by the long polar winter (Søvik et al. 2003). However, the between-boxes variation in development in the A97 microcosms on 1 July indicates that the synchronized quiescence is partly regulated by primer pheromones (Leinaas 1983). Pheromone secretions from the opisthosomal gland of oribatid mites have been described in recent publications (Raspotnig and Krisper 1998; Raspotnig et al. 2001). In the oribatid mite *Archegozetes longisetosis*, Haq (1982) observed that a few juveniles would initiate quiescence, and if disturbed, moulting would also be delayed in the other juveniles in the culture.

The synchronized quiescence might be connected to the observed aggregation behaviour of pre-moult juveniles. Aggregations of quiescent juveniles were observed in the field (Søvik et al. 2003) and also exist in the antarctic *Alaskozetes antarcticus* (Block and Convey 1995) and *Maudheimia wilsoni* (Marshall and Convey 1999), and similarly to *Ameronothrus lineatus*, *Alaskozetes antarcticus* moults synchronously in early summer (Convey 1994). Moreover, group moulting has been noted in laboratory cultures of lower latitude species (Woodring and Cook 1962; Haq 1982; Ramani and Haq 1988; Honciuc 1996). Aggregations may create optimum temperatures for moulting by increasing absorbed insolation due to the dark coloration of the solid mass of mites, hence accelerating development (Haq 1982; Block and Convey 1995). They may also be an adaptation for surviving inundation in the littoral habitats of *Ameronothrus lineatus*.

Juvenile development varied within instars, shown by the number of moults in the larval cohort, which varied from none to two. Thus, while quiescence following winter was synchronized, development during the rest of the summer, including the second moult, was less so. Our data suggest a similar developmental pattern for the nymphs, but due to inaccuracies in stage determination by size, this is less certain. Variation in developmental rate within juvenile life stages has been observed in other oribatid species (Webb 1977; Luxton 1981a; Schatz 1985; Convey 1994) and may depend on environmental conditions such as temperature (Stamou 1989) and food.

Rate of development decreased with ontogeny, shown by the decreasing number of immatures from larvae to deutonymphs moulting twice during summer 1998 (Fig. 5). An increasing duration of the juvenile stages with ontogeny has been observed in many oribatid species (Luxton 1981a; Taberly 1988; Stamou 1989; Enami 1992; Marshall and Convey 1999). The suggested sex-dependent tritonymph-to-adult developmental rate

seems to occur also in temperate *Ameronothrus lineatus* populations, where a male surplus in spring (Schubart 1975) suggests an earlier male moulting and hence faster male development. The large size difference between males and females (Søvik et al. 2003) may account for this. We do not know of any previous accounts of gender-specific developmental rates in oribatid mites.

The developmental pattern of the S98 cohorts, which experienced a lower temperature sum than the A97 juveniles, may be representative of a more normal Svalbard summer, implying that juvenile instars of arctic *Ameronothrus lineatus* have a duration of approximately 1 year. Females start larvipositing the second adult summer (Søvik and Leinaas, submitted), which gives a generation time, larva-to-larva, of ca. 5 years. The antarctic *Alaskozetes antarcticus* has a similarly long life cycle (Convey 1994). In contrast, temperate populations of *Ameronothrus lineatus* have a generation time of 1 year with virtually all adults dying before their first winter (Bücking et al. 1998). Most temperate oribatid species have life cycles lasting 1–2 years (Luxton 1981a, b; Norton 1994).

The prolonged life cycle may be explained by an adaptive timing of moulting to the warmest part of the arctic summer, with each juvenile being unable to moult more than once per season due to climatic constraints (Søvik et al. 2003). Each active stage will then be prolonged in terms of degree-days relative to temperate populations. However, the difference between the A97 and S98 cohorts also reveals a flexible life cycle, with juveniles taking advantage of favourable conditions by completing up to two moults during one season. Thus, given a couple of warm summers, some specimens may complete development in only 3–4 years. On the other hand, as some juveniles postpone moulting and females reproduce for 2–3 years (Søvik and Leinaas, submitted), short and cold summers may extend the generation time to 6–8 years. Owing to the high juvenile survival, such extensions do not involve serious costs. The long and flexible life cycle of *Ameronothrus lineatus* makes the species well suited to the natural variation and unpredictability of arctic climates.

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