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OBSERVATIONS ON OVOVIVIPARITY AND MIXED-PARITY MODE
IN ARCTIC POPULATIONS OF AMERONOTHRUS LINEATUS
(ACARI, ORIBATIDA)

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(Accepted May 2003)

OVOVIVIPARITY,
MIXED-PARITY MODE,
ARCTIC,
INFLUENCE OF TEMPERATURE,
AMERONOTHRUS

SUMMARY: The oribatid mite *Ameronothrus lineatus* (Thorell, 1871) is ovoviviparous in the high Arctic, i. e., larvae hatch from the eggs within some hours after deposition. Earlier all *Ameronothrus* species have been considered larviparous, which implies that larvae hatch from the eggs inside the female. Proving ovoviviparity requires laboratory studies where newly deposited progeny are observed. Culturing congeneric species may reveal that *A. lineatus* is not the only ovoviviparous *Ameronothrus* species. Observations of cultures of *A. lineatus* showed that occasionally eggs with incomplete larval development were deposited. These eggs were observed at all constant laboratory temperatures (5-21°C), but most of them were found at 5°C. The majority of the eggs dried without any further development taking place, but 3 (out of 61) successfully hatched after 8-12 days at 15°C. This is the first record of mixed-parity mode in an ovoviviparous oribatid mite.

INTRODUCTION

The majority of oribatid mites deposit eggs. In addition to oviposition two other less common modes of reproduction are also found: prelarviposition and larviposition (NORTON, 1994). In prelarviposition eggs are retained throughout embryogenesis and deposited as prelarvae. The oribatid prelarva is an inactive and degenerate stage, which does not hatch from the egg (NORTON, 1994; WALTER & PROCTOR, 1999). Further retention of the progeny until the larval stage is called larviposition. HAQ *et al.* (1991) distinguished between two different kinds of larviposition. Larvae may either hatch from the eggshell inside the mother's body and are then depo-

sited (true larviparity or viviparity), or larvae may hatch immediately after deposition (ovoviviparity). Strictly speaking, in ovoviviparity progeny are still in the prelarval stage at deposition as the larva has not yet emerged from the prelarval cuticle. However, as opposed to prelarviposition where progeny are deposited as legless blobs within the eggshell, ovoviviparous species deposit fully developed larvae enclosed by the egg membrane. It is useful to distinguish between these two modes of reproduction because of the different amount of time before hatching. Time from deposition to hatching may vary from hours in ovoviviparous mites (MITCHELL, 1968; pers. obs.) to many days in prelarviparous species (WEBB, 1977).

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Ovoviviparity is not uncommon in mesostigmatid and astigmatid mites (OWEN, 1956; MITCHELL, 1968; EVANS, 1992: Chapter 10; WALTER & PROCTOR, 1999: Chapter 4), but has rarely been described in oribatid mites. However, KURIKI (1993) showed that *Trhypochthoniellus setosus* Willmann, 1928 is ovoviviparous, and SHALDYBINA (1968) and HAQ *et al.* (1991) noted that in the oviparous *Sphaerozetes orbicularis* (C. L. Koch, 1835) and *Scheloribates fijiensis* Hammer, 1971, larvae sometimes hatched from the eggshell immediately after deposition. In addition to demonstrate ovoviviparity, *S. orbicularis* and *S. fijiensis* represent the only two reliable records of mixed-parity mode in oribatid mites (SHALDYBINA, 1968; NORTON, 1994). Viviparity (true larviparity) can be ascertained with certainty if larvae with extended appendages are observed within females (WALLWORK, 1967, illustration p. 385). However, unborn larvae within an egg membrane do not prove ovoviviparity, as the possibility that the larvae would have subsequently hatched inside the female cannot be excluded. To prove ovoviviparity it is necessary to rear mites and observe newly deposited progeny. In most studies such detailed observations are lacking, and consequently, species have been labelled viviparous when in fact they might have been ovoviviparous.

Ameronothrus is a holarctic genus with most species inhabiting marine littoral regions and estuaries (SCHULTE & WEIGMANN, 1977). Larviparity seems to be an ancestral (plesiotypic) trait in *Ameronothrus* (SCHUBART, 1970, 1975; WEIGMANN & SCHULTE, 1975; PUGH & KING, 1986; TILREM, 1994; BÜCKING *et al.*, 1998), and this might be correlated with the aquatic and semiaquatic mode of life of included species (NORTON, 1994). The distributions of *A. lineatus* (Thorell, 1871), *A. maculatus* (Michael, 1882), *A. lapponicus* Dalenius, 1963, *A. nigrofemoratus* (L. Koch, 1879) and *A. marinus* (Banks, 1896) stretch into higher latitudes (> 65° N) (SCHULTE, 1979; SCHULTE *et al.*, 1975; DANKS, 1981), but on the high-arctic archipelago of Svalbard only *A. lineatus* has so far been found (COULSON & REFSETH, in press). During a comprehensive study focusing on population dynamics and life history of *A. lineatus* on Svalbard detailed observations on parity were made. The present paper reports these observa-

tions and discusses their possible adaptive significance.

MATERIALS AND METHODS

In the present study, the term “egg” is used to denote an egg proper, irrespective of the stage of development within the egg membrane (embryo, prelarva or fully developed larva), while “egg stage” is used to denote the embryonic stage of development. Fully developed larvae within eggs are referred to as “larvae”, even though they are still enclosed by the prelarval cuticle, as well as the egg membrane. In *A. lineatus* the prelarva is only a layer of cuticle within the eggshell (SCHUBART, 1975), and the egg and prelarval stages can only be distinguished by close inspection under the microscope and were not attempted separated in this study.

Inspection of the progeny of a large number of field collected gravid females was carried out during summers 1997 and 1998. Two habitats on West Spitsbergen were sampled: a saltmarsh in the valley Adventdalen (78° 10' N 15° 30' E) and smooth mud flats coated by cyanobacteria in the bay Colesbukta (78° 5' N 14° 57' E) (SØVIK *et al.*, 2003). The Adventdalen mites were extracted from the organic soil over eight days using a high-gradient extractor (MACFADYEN, 1961), while on the cyanobacteria surface all mites were visible and could be sampled by hand using a soft brush. All sampled females were cleared in lactic acid and the progeny observed.

To study the reproductive biology of *A. lineatus* in more detail, approximately equal numbers of adults were in 1999 cultured at four different constant temperatures (5, 10, 15 and 21°C), from ecdysis until death. Newly moulted adults (70 females, 30 males) were sorted into four culture plates containing pieces of the cyanobacteria layer on a mixture of charcoal and plaster of Paris (1:8). The cultures were kept at 100 % humidity and checked approximately once a week. Deposited progeny were observed and removed. Yellow, transparent eggs with no sign of larvae were placed in separate culture boxes at 15° C to check if hatching occurred. Dead females were cleared and progeny observed. Observations and rearing of eggs with incomplete larval development were also

made in several other laboratory cultures of *A. lineatus* (from 1999 to 2001), where a total of 251 adults were reared for 3-10 months. On a couple of occasions cultures were observed two days in a row, which enabled estimation of time from deposition until hatching.

RESULTS

During summers 1997 and 1998 a total of 5788 adults were collected from the two study sites. In Adventdalen and Colesbukta respectively 55 and 67 % were females. Gravid females were found on all sampling dates (SØVIK *et al.*, 2003). Larvae carried by females were easy to distinguish from the egg stage and prelarvae (FIG. 1). The former were nearly always dark brown due to the larval cuticle, and larval features were clearly visible, while the latter were transparent. All larvae observed inside females had the appendages pressed closely to the ventral surface and it was often possible to observe the egg membrane, within which the larvae were confined. Some of the sampled females carried a fully developed larva in their long ovipositor, and the egg membrane enclosing the larva was clearly visible. Dark brown eggs containing larvae were sometimes observed in the

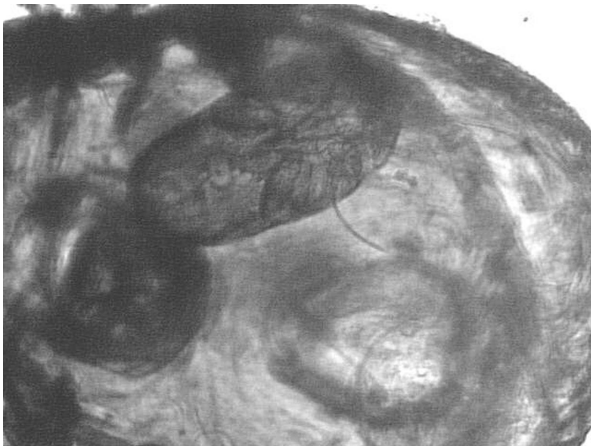


FIG. 1: A female *A. lineatus* carrying a larva (within the egg membrane) and two embryos and/or prelarvae (in the right side of the photo). The larva has the appendages pressed closely to the ventral surface. The genital opening (left) and anal opening (right) can be seen in the lower part of the photo as rounded, dark areas.

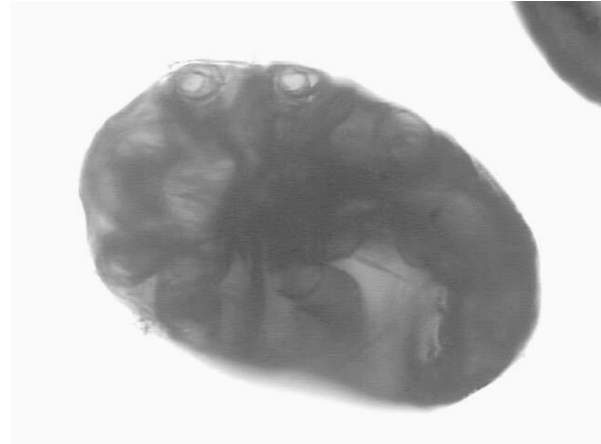


FIG. 2: A newly deposited larva still enclosed within a clearly visible egg membrane.

extracted Adventdalen samples (FIG. 2). Similarly, in the laboratory cultures, newly deposited dark brown eggs were observed on the cyanobacteria surface. Observations of newly deposited hatched larvae on the second of two consecutive days showed that hatching occurred within hours after deposition. However, the exact time from deposition until hatching was not recorded.

A total of 61 yellow, transparent eggs with no sign of larvae were deposited in all the studied cultures. In the culture plates at four constant temperatures, 32 eggs with incomplete larval development were observed, compared with 481 deposited larvae. The majority of eggs with incomplete larval development (21) were found at 5°C. It was not determined whether the yellow eggs were at the egg or prelarval stage. More or less all shrivelled and dried without any further development. However, in five of them larvae developed, seen by a darkening of the eggs, and three hatched after 8, 10 and 12 days respectively. The larvae survived for several weeks, but none moulted to protonymphs.

DISCUSSION

The field and laboratory observations clearly show that *A. lineatus* is an ovoviviparous species, where females deposit eggs out of which larvae hatch shortly after. Earlier works have described the species

as larviparous, probably in the sense of viviparity (SCHUBART, 1975; BÜCKING *et al.*, 1998), which is likely due to the fact that no one has previously studied the reproductive biology of *A. lineatus* in detail, using both cultures and extensive field sampling. As larviparity seems to be a plesiotypic trait of *Ameronothrus*, culturing congeneric species may reveal that *A. lineatus* is not the only ovoviviparous species in this genus.

The fact that most of the transparent, yellow eggs died before hatching suggests that they may represent a form of abortion. This is supported by the fact that the majority of eggs with incomplete larval development in the cultures at 5–21° C were observed at 5° C, the temperature shown to be the least optimal for reproduction in *A. lineatus* (pers. obs.). Thus, a low constant temperature often prevents ordinary embryonic development, resulting in too early deposition of progeny. However, some of these eggs actually finished embryonic development outside the mother's body. Oviposition (or perhaps prelarviposition) in the ovoviviparous *A. lineatus* is the first record of mixed-parity mode in a larviparous oribatid mite. Thus, *A. lineatus* reproduces either by laying eggs with fully developed larvae which hatch immediately (ovoviviparity) or, occasionally, by laying eggs with incomplete larval development which hatch several days to weeks later, depending on temperature (oviparity). The other two reliable records of mixed-parity mode in oribatid mites are the already mentioned oviparous *Sphaerozetes orbicularis* and *Scheloriabates fijiensis*, which occasionally deposit eggs that hatch immediately (SHALDYBINA, 1968; HAQ *et al.*, 1991). According to NORTON (1994), conflicting reports also exist concerning *Nothrus palustris* C. L. Koch, 1839, where some authors have found fully developed larvae in females, while the species seems to be prelarviparous in other parts of its distribution. Some mesostigmatid mites have also been reported to show mixed-parity mode (MITCHELL, 1968; FILIPPONI, 1965) and some of these are ovoviviparous mites occasionally ovipositing.

The low proportion of eggs developing and hatching, and the fact that none of the hatched larvae survived may indicate that the observed mixed-parity mode is of minor importance in the reproductive biology of *A. lineatus*. On the other hand, the low

survival could also result from unsatisfactory culture conditions. For instance, the hatched larvae were reared alone, and low survival at low densities has been reported in oribatid species (STAMOU & ASIKIDIS, 1989). If this is the case deposition of eggs may represent an alternative reproductive strategy at very low temperatures.

Advantages of larviparity (viviparity/ovoviviparity) versus oviparity have been discussed by several authors (FASHING, 1975; HAQ *et al.*, 1991; NORTON, 1994). Deposited eggs are vulnerable to predation and desiccation (FASHING, 1975; BLOCK & CONVEY, 1995) and egg retention protects the progeny throughout embryogenesis. Furthermore, there seems to be a correlation between larviparity and an aquatic mode of life (FASHING, 1975; NORTON, 1994), where larviposition prevents eggs being washed away by tidal action or rapidly moving water. Considering that mixed-parity mode seems to be a rare life history trait among oribatid mites, one might ask what the advantages to arctic *A. lineatus* of oviparity versus larviparity could be. Furthermore, under what circumstances might this mixed-parity mode develop? FILIPPONI (1965) found food to be the most influential factor on the mode of reproduction, where plentiful food favoured oviparity and food limitation viviparity. In the present study, the mode of reproduction was influenced by temperature, with low temperatures leading to oviparity.

Laboratory studies of *A. lineatus* have shown that at a constant temperature of 5° C embryonic development was extremely slow, where the first larvae were deposited in the third adult summer (pers. obs.). Moreover, approximately half of the progeny at this temperature (56 out of 118) were either deposited as eggs with incomplete larval development or were never deposited as the mother died. Experimental field studies of *A. lineatus* have shown adult winter survival to be significantly lower than juvenile winter survival (Søvik and Leinaas, in press). This is in accordance with results from cold hardiness experiments on the antarctic *Alaskozetes antarcticus* (Michael, 1903) and the alpine *Ameronothrus lapponicus* where juveniles possess a higher degree of low temperature tolerance than adults (YOUNG & BLOCK, 1980; HANSEN, 2000). Similarly, SUGAWARA *et al.* (1995) found that eggs of another antarctic oribatid

mite, *Antarcticola meyeri* Wallwork, 1967, had a significantly lower supercooling point than other life stages. Thus, a possible advantage of oviparity as opposed to larviparity in an extreme environment with very low summer temperatures would be that the necessarily slow embryonic development would be less dependent on female winter survival. At high latitudes *A. lineatus* becomes less tied to the marine tidal zone (SCHUSTER, 1966). On Svalbard the species has been found underneath rocks 500 m from the shore and 100-150 m above sea level (pers. obs.). Freed from tidal stress and the risk of eggs being washed away, it seems possible that ovoviviparity may develop into mixed-parity mode in arctic populations of *A. lineatus* inhabiting the most extreme environments.

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