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THE BIOLOGY OF HYPOASPIS ACULEIFER (CANESTRINI) (MESOSTIGMATA) :
IS THERE A TENDENCY TOWARDS SOCIAL BEHAVIOUR?

BY M. B. USHER and P. R. DAVIS*

ABSTRACT: In the absence of males, females of Hypoaspis aculeifer lay eggs which develop only into males. However, in the presence of males, the eggs develop into both sexes. The species is therefore presumed to be arrhenotokous (haplodiploid).

Laboratory experiments indicated that (I) H. aculeifer is not cannibalistic except under extreme conditions of hunger, (II) there is no evidence of oophagy, (III) the mite does not 'overkill' its prey, (IV) with large Sinella coeca as prey the efficiency of capture increases with predator density whilst with easily caught prey the efficiency decreases, and (V) large Hypogastrura denticulata reduce the predator's longevity and fecundity.

The criteria for a species to reach the eusocial threshold (Wilson, 1971) are reviewed. Although several generations of mites can overlap, there is neither co-operative brood care nor the existence of a reproductive caste. There is, however, apparently no harassment of the young. It is suggested that mites in the family Dermanyssidae, especially the species associated with vertebrate nests, are intermediate subsocial.

RESUME: En l'absence de males, les femelles d'Hypoaspis aculeifer depoissent des oeufs qui se developpent tous en males. Toutefois, en presence de males, les œufs se developpent dans les deux sexes.Cette espèce est donc presumee être arrhenotoque (haplodiploïde).

Les experiences de laboratoire ont montré que (I) H. aculeifer n'est pas cannibale exception faite d'extrême condition de famine, (II) il n'y a aucune manifestation d'oophagie, (III) l'acarien ne tue pas de proies au delà de ses besoins, (IV) avec pour proie le grand Sinella coeca l'efficacité des captures s'accroît avec la densité des prédateurs tandis qu'avec des proies faciles à prendre cette efficacité décroît, et (V) le grand Hypogastrura denticulata réduit la longévité et la fécondité du prédateur.

Les critères pour qu'une espèce ait atteint le statut eusocial (Wilson, 1971) sont examinés. Bien que plusieurs générations de l'acarien se recouvrent, il n'y a ni coopération des soins à la progéniture, ni existence d'une caste de reproducteurs. Il n'y a, toutefois, apparemment aucun harassment des jeunes. Il est suggéré que les acariens de la famille des Dermanyssidae, en particulier les espèces associées aux nids des Vertébrés, seraient des subsociaux intermédiaires.

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Hypoaspis aculeifer (Canestrini) is a widespread and common soil mite, which is placed either in the family Laelaptidae (KEVAN & SHARMA, 1964; IGNATOWICZ, 1974) or in the family Dermanyssidae (EVANS & TILL, 1966). It has been collected throughout the European and North American Continents (BREGETOVA, 1956; KARG, 1961; EVANS & TILL, 1966), and from a wide variety of different habitats. It is generally believed to be a polyphagous predator. During laboratory studies of its predatory behaviour in cultures of two species of Collembola, Sinella coeca (Schott) and Hypogastrura denticulata (Bagnell), DAVIS (1978) observed its reproductive and cannibalistic behaviour. These observations have led to speculation that H. aculeifer, and possibly other related species, demonstrate certain population phenomena that are characteristic of subsocial arthropods.

Previous studies on H. aculeifer indicate that it reproduces sexually. IGNATOWICZ (1974) makes the positive statement that eggs are only laid by adult, fertilized females. KEVAN & SHARMA (1964) investigated the fecundity and described the developmental stages, but they experimented with recently fertilised young females. Neither study detected parthenogenetic reproduction, although different forms of parthenogenesis (arrhenotoky, thelytoky, deuterotoky, gynogenesis) occur widely in the Acarina (OLIVER, 1971). OLIVER states 'arrhenotoky occurs in the Mesostigmata, Prostigmata and Astigmata...; when present it operates in many closely related species as the major type of reproduction in certain genera, sub-families or families', and he quotes several examples of arrhenotoky in both the Laelaptidae and Dermanyssidae. If OLIVER’s assertion about familial correlation in reproductive behaviour is correct, then it is at least possible that H. aculeifer would reproduce arrhenotokously. Arrhenotoky, or haplodiploidy, occurs when fertilized eggs develop into females (diploid individuals) and unfertilized eggs into males, (haploid individuals).

Such a reproductive structure is important in considering the development of a social structure in a species. H. aculeifer was an extremely easy predatory mite to culture in the laboratory. Most Mesostigmatid mites do not persist in culture since either they tend to 'overkill' the prey population (see, for example, HARRIES, 1974) and then die of starvation, or they are excessively cannibalistic, appearing to prefer their own juveniles to the available prey. Sometimes they demonstrate both of these characteristics. However, neither of these traits was seen in cultures of H. aculeifer, which therefore approaches the condition of being a satisfactory laboratory invertebrate predator.

**Materials and Methods**

Microarthropods were extracted by Tullgren funnel from soil samples taken from Wharram Quarry Nature Reserve (National Grid Reference SE857654), a chalk grassland site in the Yorkshire Wolds. About twenty species of Mesostigmata were collected, and all were used to initiate laboratory cultures. These initial cultures indicated that H. aculeifer was the most amenable to laboratory culture. It readily preyed upon two species of Collembola, S. coeca and H. denticulata, which had also been extracted from a chalk grassland site in the Yorkshire Wolds (LONGSTAFF, 1974), and which had been maintained in the laboratory for several years. Both S. coeca and H. denticulata are thought to feed naturally upon fungi and other micro-organisms, and they thrive in the laboratory when fed on dried baker's yeast pellets. It was found that one grain of yeast, sifted to be between .5 mm and .8 mm diameter, per five individuals per two week period, would neither starve the Collembola nor result in excessive fungal growth on the yeast which otherwise would 'clog' the culture floor.

The plastic culture vessels used were 5 cm in diameter and 2.5 cm in depth. They contained a floor of Plaster of Paris and charcoal (mixed in a 9:1 ratio), cast to a depth of approximately 0.5 cm, which was kept moist with a few drops of distilled water every week. The culture vessels
were sealed with a transparent clingfilm. Photographs of the cultures were taken with a Zenza Bronica 52 camera, with a 75 mm lens reversed, utilising diffused top lighting and bright side lighting. This system made accurate population censusing possible, and resulted in a minimum of disturbance of the cultures.

RESULTS

Pathogenesis

Seventy-two pre-adult individuals of Hypoaspis aculeifer (eggs, larvae, protonymphs and deutonymphs) were removed from mass laboratory cultures, and each was individually isolated in a culture vessel, in darkness, at a constant temperature of 24°C. Thirty of these moulted successfully into females, which were kept isolated for a further six weeks, after which there were 24 survivors. The eggs laid during this period were removed daily, and transferred individually to new culture vessels. After the six weeks the cultures which still contained live females were randomly assigned to two groups. In the first group the females remained isolated from other mites, whilst in the second group two males were introduced to each culture vessel. From all of the culture vessels the eggs continued to be removed daily and transferred to individual cultures. The removal of eggs was continued until all the females were dead. The results of this experiment are shown in Table 1.

<table>
<thead>
<tr>
<th>Female age (weeks)</th>
<th>Males</th>
<th>Number of females cultured</th>
<th>Number of eggs laid</th>
<th>Progeny surviving to adulthood</th>
<th>Number of females</th>
<th>Number of males</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-6 None</td>
<td>30</td>
<td>140</td>
<td>43</td>
<td>0</td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7 and more Present</td>
<td>12</td>
<td>86</td>
<td>42</td>
<td>0</td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7 and more Previously present, now both dead</td>
<td>7</td>
<td>16</td>
<td>4</td>
<td>2</td>
<td>67</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

In all of the cultures in which the females were isolated the eggs developed only into male offspring, although there was a mortality of 62% during development. However, when males were present, or when males had been present and had subsequently died, the eggs developed into adults of both sexes (the mortality was 45%). Differential mortality of haploid and diploid individuals has been considered by Smith & Shaw (1980). The results in Table 1 indicate that virgin females from this Yorkshire stock are fecund, but that they only produce male offspring, whereas both sexes are produced by females that have had experience of males. H. aculeifer would therefore appear to be arrhenotokous: proof of arrhenotoky would be provided by a study of the chromosome number in the two sexes, but, in common with other work on mature mites (Oliver, 1971), adequate preparations of chromosomes have proved impossible to make.

Cannibalism

Although arrhenotokous reproduction partially explains the success of H. aculeifer in laboratory cultures (Davis, 1978), it was also remarkable that cannibalism was not observed when alternative prey were available. Adults were observed to eat immature stages only after weeks of starvation, and then it could not be ascertained whether this was the removal of corpses of the young stages or an active form of cannibalism. Oophagy was never suspected since the number of eggs in cultures with adults never decreased except when the eggs hatched. These observations strongly contrast with those of other predatory soil mites from the same environment: Machrocheles spp. were frequently observed to cannibalise their own young, and Pergamasus longicornis (Berlese), from a Wolds grassland site, appeared to prefer eating its own juveniles to the species of Colleme-
bola which were offered as possible prey (HARRIS, 1974).

In order to ensure that the apparent absence of cannibalism was a real feature of this species, and not merely unobserved because of a relatively low rate of cannibalism, small fixed numbers of mites were isolated in standard culture vessels in darkness at 16°C and were observed weekly over a 9-week period. During this period any eggs that were laid were removed, any dead mites were replaced, and any juveniles that had moulted to adulthood were also replaced with juveniles. Mixed species of Collembola were provided as prey, and their population density was kept at the relatively low level of 20 per culture.

In the experimental design three classes of mites — females, males and juveniles — were recognised. Two individuals of each class were cultured with four individuals of the same class or the smaller classes. Thus, the six combinations were six females, two females with four males, two females with four juveniles, six males, two males with four juveniles, and six juveniles. All of these combinations were replicated three times. A summary of the data from this experiment, and an analysis of variance of the full results, are shown in Tables 2 and 3.

The results indicate that the death rate of any class is not significantly altered by the presence of any other class when the alternative prey, Collembola, are present. However, the analysis of variance, Table 3, indicates that the mean death rate of the classes differ, since that of the juveniles is greater than that of either of the adult classes, which are not significantly different from each other. The lack of significance either of the class 'cannibalising' or of the interaction terms suggests that cannibalism does not occur. If it did occur then one would expect the two adult classes to induce larger death rates in the juveniles, or at least that the females would have a significantly larger effect on death rates since they are larger in size than the males. An interesting variance ratio in Table 3 is that of time, which has a probability between 0.10 and 0.05. The data indicated that the death rate increased slightly with time, probably because of an ageing effect of the mites that were included in this experiment.

### Table 2. The average mortality per week of three classes of H. aculeifer in the presence of the same or another class of the mite (classes are male, female and juvenile), averaged over the three replicates and over the 9-week period. The main diagonal elements of this table are means over the six individuals of the class, whilst in the upper right the elements are means over four individuals and in the lower left they are means over two individuals. The standard error for the table entries, from the analysis of variance in Table 3, is ± 0.011.

<table>
<thead>
<tr>
<th></th>
<th>female</th>
<th>male</th>
<th>juvenile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>0.07</td>
<td>0.19</td>
<td>0.25</td>
</tr>
<tr>
<td>Males</td>
<td>0.09</td>
<td>0.06</td>
<td>0.18</td>
</tr>
<tr>
<td>Juveniles</td>
<td>0.11</td>
<td>0.04</td>
<td>0.27</td>
</tr>
</tbody>
</table>

### Table 3. The analysis of variance of the data of the cannibalism experiment, shown in summary in Table 2. None of the interaction terms was statistically significant, so they have been combined with the error sum of squares in the analysis.

<table>
<thead>
<tr>
<th>Source</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>Variance ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class 'cannibalised'</td>
<td>2</td>
<td>0.056</td>
<td>0.028</td>
<td>8.48 (P &lt; 0.001)</td>
</tr>
<tr>
<td>Class 'cannibalis ing'</td>
<td>2</td>
<td>0.004</td>
<td>0.002</td>
<td>0.61</td>
</tr>
<tr>
<td>Time</td>
<td>8</td>
<td>0.044</td>
<td>0.006</td>
<td>1.67</td>
</tr>
<tr>
<td>Interaction and error</td>
<td>230</td>
<td>0.759</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>242</td>
<td>0.863</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Predation**

DAVIS (1978) attempted to build a three species population model based on the data from cultures of *H. aculeifer, S. coeca* and *H. denticulata*. He used a factorial design which included three classes of *H. aculeifer* (female, male and juvenile) and three sizes (small, medium and large) of the two prey species. This gives 18 predator-prey combinations, each of which was repeated 27 times due to the different levels of prey density, predator density, and a three-fold replication of the whole experiment. Before any of these experimental cultures were set up, the mites were removed from stock cultures and kept isolated for 24 hours. An individual experiment was then begun by counting into culture vessels the appropriate numbers of both prey and predator, and
the culture was photographed after 4, 8 and 12 days. At 4 and 8 days the prey were replenished from stock cultures according to a fixed replenishment regime (for details, see DAVIS 1978), and after 12 days the predator was added to a back-up culture and was not re-used in any further experiments. The 18 predator-prey combinations of the experiment were randomised in time over a 13-week period. Any mite that died during an experiment, or any juvenile that moulted to adulthood, was replaced. All eggs were removed.

Of the two species of prey used in the experiments, S. coeca is the larger and more active, and it has a well developed furcula that is used for leaping: adult individuals are larger than adult female H. aculeifer. H. denticulata is smaller, moves more slowly, and appears to rely on chemical rather than on mechanical defences against predation: it is, therefore, the easier prey for all classes of H. aculeifer to catch, but it may prove distasteful. Casual observation indicated that whereas solitary female mites tend to predate small prey, when several females were present there was greater predation on the larger, more active prey. Several mites could be observed to feed off a large, dead, S. coeca, although the method of catching this large prey was never observed. The data on the size of prey that were caught during the experiment are shown in Table 4.

First, these data indicate that the predators kill fewer large prey than small prey. This would be expected with a predator that eats all its prey and does not ‘overkill’. Secondly, an increase in predator density when preying upon small and manageable prey reduces the predator efficiency, presumably due to mutual interference between the mites (HASSELL & VARLEY, 1969; BEDDINGTON, 1975). This situation appears to be reversed for the large, active prey (S. coeca) since the mean rate of capture, as a measure of predator efficiency, increases by 50 percent from .10 to .15 prey per predator per day. Even with medium sized S. coeca the predator efficiency remains more or less constant with predator density.

Data on the fecundity of the female mites included in these experiments are difficult to interpret since there was considerable variation between individual mites. However, when female H. aculeifer was predating small or medium sized S. coeca the mean fecundity was 0.12 eggs per female per day, and this increased to a mean of 0.21 eggs per female per day when predating large S. coeca. The maximum fecundity, 0.31 eggs per female per day, was recorded for the greatest predator density (8 mites per culture) feeding on large S. coeca. In contrast, the fecundity of H. aculeifer when predating small or medium sized H. denticulata was 0.17 eggs per female per day, which decreased to 0.02 eggs per female per day when predating large H. denticulata. Analysis of variance indicated that large H. denticulata both inhibited oviposition in H. aculeifer and reduced the longevity of adult mites. Observational data of both H. aculeifer and Pergamasus longicornis indicate the effectiveness of the chemical defence mechanism of H. denticulata: after attempting to make an attack the mite would back away from the Collembola dragging its chelicerae on the substrate, apparently trying to wipe them.

### Table 4

<table>
<thead>
<tr>
<th>Predator density</th>
<th>Prey</th>
<th>Sinella coeca</th>
<th>Hypogastra denticulata</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>s m l</td>
<td>s m l</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>.81 .31 .10</td>
<td>1.31 .82 .12</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>.67 .33 .11</td>
<td>1.21 .53 .05</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>.51 .36 .15</td>
<td>1.05 .43 .07</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>.66 .33 .12</td>
<td>1.19 .59 .08</td>
<td></td>
</tr>
</tbody>
</table>
DISCUSSION

The results from each of these three experiments — on parthenogenesis, on the lack of cannibalism, and on the predatory behaviour in the face of large prey species — indicate that *H. aculeifer* is an unusual mite. The observations invite not only speculation about the organisation of the populations of this predator, but also speculation about the roles of reproductive strategy and predatory behaviour in the evolution of social structures in the arthropods.

First, what are the implications of arrhenotoky? An introduction to this form of parthenogenesis in the spider mites (family Tetranychidae) by HELLE (1965a, 1965b) highlights several important points. First, the diploid females are more closely related genetically to the hemizygous male offspring than to their daughters. Second, because of the haploid nature of the male, lethal or, to a lesser extent, any disadvantageous genes are lost rapidly from the population, whilst favourable alleles are more rapidly fixed. This can, however, lead to unusual sex ratios (SMITH & SHAW, 1980). Finally, because of the observed intrapopulation variability, it was suggested that there might be a high spontaneous mutation rate.

When these genetic implications are coupled with the longevity of the individuals (found by experiment to be 120-130 days for males and 290-450 days for females) and with the relatively short developmental period from egg to adult (in the laboratory about 40-55 days), it can be seen that several generations can exist in one place at one time. The existence of overlapping generations is one of the three criteria which characterise eusocial behaviour (see WILSON, 1971; WILSON, 1976; and OSTER & WILSON, 1979): in fact this one character alone is sufficient to define *H. aculeifer* as 'intermediate subsocial' (WILSON, 1971, Table 2-2).

Studies by HARRIS (1974) and HARRIS & USHER (1978) have indicated that *Pergamasus longicornis*, a common predatory mite that has a normal form of sexual reproduction, is a 'greedy' predator since it kills more prey than it can eat and since it cannibalises smaller individuals of its own species often in preference to eating alternate prey. Observational studies on other species of Mesostigmata indicate that such predatory behaviour is common. However, if cannibalism occurred in an arrhenotokous species with overlapping generations, it is possible that females would eat their male descendents with which they are genetically identical. Indeed, it is very likely that such genetically related individuals will come in contact with each other since the mite lives in the soil, a medium in which dispersal is difficult. There are no known dispersal phases in *H. aculeifer*, and the species is not recorded as being phoretic. Genetically, there would therefore appear to be disadvantages in being both arrhenotokous and cannibalistic. In *H. aculeifer* cannibalism is either absent or it is confined to abnormal situations when the mites have been starved for a considerable length of time.

The lack of cannibalism does not imply that a second of the three criteria for eusociality has been fulfilled: the criterion is in fact the existence of co-operative brood care. However, the efficiency of *H. aculeifer* when in the presence of large, suitable prey can increase with increasing population density (Table 4). Large *S. coeca* would certainly be too large for a single *H. aculeifer* to capture and kill, whereas small *S. coeca* can be caught and eaten. The observation of several mites feeding from one dead *S. coeca* body also suggests that some form of cooperation between adult individuals of *H. aculeifer* is possible. It should, however, be stressed that the possibility of 'pack hunting' and 'communal eating' is far from co-operative brood care, but it is certainly of unusual occurrence in the predatory Mesostigmata. Thus, using WILSON's (1971) terminology, there is a movement from the species being 'intermediate subsocial I' to being 'intermediate subsocial II'.
The third criterion for eusociality is the existence of reproductive castes: there is no evidence at all for caste differentiation in *H. aculeifer*. However, the observation of Ignatowicz (1974) that parthenogenetic reproduction does not occur, and the present results that all isolated females are capable of egg laying, does suggest that within the species of *H. aculeifer* there are different reproductive races. How these races are distributed geographically, and whether individuals of both types occur together, remains unknown.

Oster & Wilson (1979) use optimization theory as a central tenet of their models of social structure, and they list some of the ecological factors which could be the focus of such optimization. It is possible that the factor of importance for small arthropod predators is the procurement of sufficient prey. *H. aculeifer* is one of the smaller species of Mesostigmatid mite in the Northern Temperate Regions. The dorsal shield of the female averages 0.68 mm in length and that of the male 0.54 mm in length (Evans & Till, 1966). Many of its potential prey species are the Collembola, which, in the Wharram Quarry environment from which *H. aculeifer* was collected, are in the range 0.8 to 4 mm long. The first instar Collembola would thus approximate to this predator in size, though often the predator would be faced by prey larger than itself. It is tempting to suggest that the co-operation suspected in laboratory cultures on a flat surface could be extrapolated to the three-dimensional soil environment in the field, and hence that the problems involved in living with larger prey may have been the factor that has taken *H. aculeifer* a small way towards the eusociality threshold.

*H. aculeifer* has not reached this threshold, but it can be considered as a subsocial arthropod. No review exists of the ecology of the Dermanyssidae, the family to which *H. aculeifer* belongs, possibly because the family is relatively unknown. However, in discussing the taxonomy of the family, Evans & Till (1965) mention the extremely wide range of "structural and biological adaptations to the variety of ecological niches they have successfully colonized ". Some species, such as *H. aculeifer*, are described as free-living inhabitants of soil and humus, whilst other species display "various degrees of association with vertebrate and invertebrate animals. Associations with other animals range from predatory species living in the nests of insects, birds and mammals to facultative and obligatory ectoparasites of the nesting-animal ".

In a study of the Siphonaptera in subterranean moles' nests (Usher, 1968), many communities of Dermanyssid mites were observed. Whilst some individuals had guts darkened with blood, the majority showed no visible gut contents and may not have been feeding directly from the moles. However, in these subterranean habitats, there is less scope for dispersal than in the soil environment inhabited by *H. aculeifer*. The reproductive strategies of these nest-inhabiting species are unknown, but if Oliver's (1971) assertion is correct, many, if not all, of them may be arrhenotoki. Since the environment of a subterranean nest is more constant throughout the year than the litter due partly to the insulating effect of the soil and partly to the presence of the homeotherm in the nest, it is likely that the nest-inhabiting mites could reproduce throughout the whole year, leading to a more predictable overlapping of generations. In these conditions it is possible that the Dermanyssid mites, occurring in dense, spatially-isolated communities, have approached the eusociality threshold more closely than *H. aculeifer*. It is in the nest-inhabiting species of this family that social behaviour in the mites is likely to have reached its highest degree of development.

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References


Paru en octobre 1983.