OBSERVATIONS ON THE EGGS AND EARLY POSTEMBRYONIC STAGES OF *STRIGAMIA MARITIMA*

Jenni Johnstone and Wallace Arthur

Ecology Centre, University of Sunderland, Sunderland SR1 3SD, UK

INTRODUCTION

Although there are more than 20 species of geophilomorph centipedes in the British Isles (Barber & Keay 1988) and more than 1000 worldwide (Lewis 1981), very little is known of their reproduction, or of their embryonic or early postembryonic development. The main reason for this is that broods of most species are very hard to find, and almost never occur in appreciable numbers within any given area. Broods brought back to the laboratory for study are often abandoned by the mother and subsequently die. In other cases, disturbance causes the mother to eat the brood. Several species will lay eggs in the laboratory if collected in the field at the right time of year (April/May). However, these also are often abandoned or eaten, especially if there is any disturbance, as there always must be if detailed observations are to be made.

The only exception known so far to the rule that geophilomorph broods are sparsely distributed and very difficult to find in substantial numbers is the coastal species *Strigamia maritima* (Leach). Thus is it no surprise that the only detailed study to date on this subject was carried out on this particular species. Lewis (1961) studied a population at Cuckmere Haven in Sussex, and gave detailed information on the location of brooding sites and the timing of developmental stages. This information is very valuable because of our general lack of knowledge about geophilomorph reproduction and early development. However, since it was restricted to a single locality on the south coast of England (with a small amount of data from another site on the south coast (Lewis 1962)), the question remains of the extent to which there is variation between populations, particularly those living in widely separated areas under quite different environmental conditions. Here, we examine this issue by providing information on a population of *S. maritima* at Whitburn, Tyne and Wear, more that 400 km to the north of Cuckmere Haven, and also a little information on two Scottish populations. We also give size data for adolescens I specimens collected from the Whitburn population and maintained in the laboratory for more than four months.

FIELD SITES AND METHODS

The main site we used consisted of a stretch of muddy cliffs and shingle some 1.5 km in length running from the northern outskirts of Sunderland up towards Whitburn. Although occasional isolated broods were found in various parts of this study site, the data presented below derive from a very small area (less than 20m long x 3m from seaward to landward). This small study area was located at about the centre of the

overall study site (grid ref. NZ 414619). It is easy to relocate as it is at the base of a flight of wooden steps leading down the cliffs.

Our two Scottish sites are at North Berwick, near Edinburgh (grid ref. NT 610845), and Brora, north of Inverness (grid ref. NC 871011). The habitats at both of these sites are rather different to Whitburn: flat rocks overlying a mixture of sand and grit (North Berwick) and a shingle bank some 2-3m in depth (Brora).

We made single visits to the Scottish sites and multiple visits to Whitburn. In each case, having located the brooding area, we removed complete broods (mother and all eggs/young) and took them to the laboratory. We noted the sizes of broods, counted segment numbers of mothers and offspring for the purpose of investigating heritability of this character (Kettle *et al.* 2002) and cultured adolescens I individuals from Whitburn for up to 20 weeks to see whether they would moult and/or grow.

These adolescens I cultures were maintained in clear plastic boxes (dimensions 14 x 8 x 5 cm) at two temperartures: 10°C and 17°C. Adult *Drosophila* (frozen, then defrosted) were provided as food on a weekly basis, and the cultures were kept humid. Males and females were cultured separately. The experiment started on 10th September 2001 and finished on 28th January 2002. Head width, body length and weight were recorded. This experiment was designed to test three things: (i) whether there might be an additional moult between those known at the beginning and end of the Adolescens I stage, something on which there has been some speculation (J.G.E. Lewis pers. comm.); (ii) whether elevated temperature can accelerate the transition to Adolescens II, which in the wild takes a considerable time - about 10 months (Lewis 1961); and (iii) whether any growth might occur in the absence of moults, given (a) the insubstantial and flexible nature of the cuticle at this early stage; and (b) the recent finding that in other moulting animals closely related to arthropods not all growth is associated with moults (Knight *et al.* 2002).

RESULTS

(a) Location, nature and size of broods in the field

At Whitburn, broods were typically found in cavities excavated from soft substrate underneath stones at a depth of 5-20 cm. At North Berwick, brood cavities were found under single flat rocks, only 5-10 cm below the surface. At Brora, the brood cavities were found in those parts of the shingle bank where stones had become embedded in a soft substrate consisting of decayed seaweed and other detritus, usually some 5-15 cm in depth. In all cases, broods were found in a very narrow band roughly 2m wide (dependent on slope), its lower border being the spring high tide mark, as indicated by the highest line of decaying seaweed.

The nature of broods is very consistent both within and between sites. The mother is invariably coiled around the eggs with her ventral surface outwards. Broods can be very close together. In the most densely packed brooding areas the distance between neighbouring broods can be as little as the diameter of a single brood (about 1 cm). However, at Whitburn broods were typically at least 10 cm apart. The number of young per brood at Whitburn varied up to a maximum of 20. The brood size frequency distribution is shown in Figure 1. We did not quantify brood sizes at the

other sites. It should be borne in mind, when interpreting Figure 1, that most broods were sampled after hatching, and the number of eggs laid may have been higher.
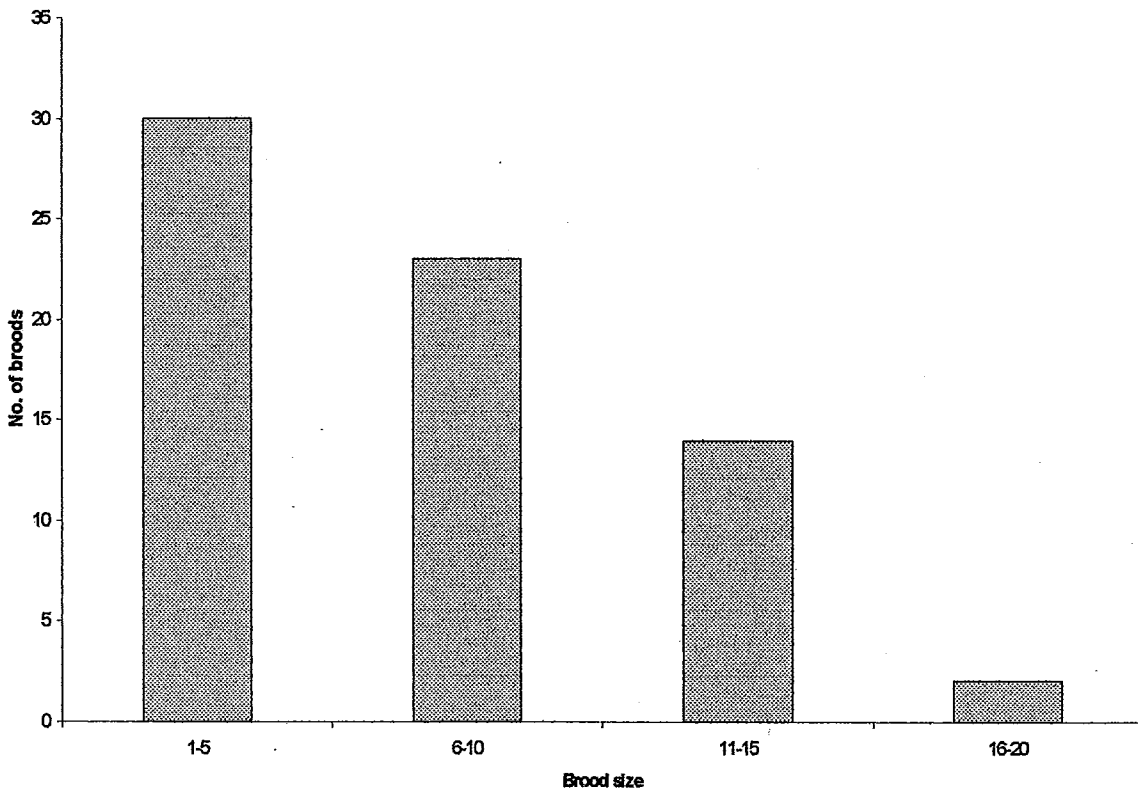

FIGURE 1

Frequency distribution of brood size in the Whitburn population

(b)   Timing of egglaying and duration of early postembryonic stages

The stages present on each sampling occasion at Whitburn are shown in Table 1, using a similar format to that of Lewis (1961) to facilitate comparison. However, even with similar formats, direct day-to-day comparison is not possible as the precise dates we used did not correspond with those used by Lewis. To get around this problem, a broader picture is presented in Table 2 with the data grouped into half-months. Since most half-months from the mid-May until mid-August were sampled in both surveys, the data are comparable at that coarser scale. No difference in timing between the two localities is discernible from Table 2, so either there is no difference at all or there is a slight difference that it is not detected with half-monthly time periods.

35

TABLE 1

STATE OF DEVELOPMENT OF BROODS AT WHITBURN 2001

Date	Broods at egg stage	Broods at peripatoid stage	Broods at Foetus stage	Broods at adolescens I stage
04 June	2			
05 July		1	9*	
16 July			7	
25 July			9	8**
30 July				8
03 August				6
13 August				18
14 August				15

*one of these broods contained 1 peripatoid along with 11 foetuses
**one of these broods contained 1 foetus along with 8 adolescens I's

TABLE 2

COMPARISON OF THE TIMING OF DEVELOPMENTAL STAGES IN POPULATIONS AT CUCKMERE HAVEN, SUSSEX AND WHITBURN, TYNE AND WEAR

Locality	Late May 16th-30th	Early June 1st-15th	Late June 16th-30th	Early July 1st-16th	Late July 17th-31st	Early August 1st-14th
Cuckmere	e	e	e/p	p/f	f/a	a
Whitburn	?	e	?	p/f	f/a	a

Note: e = egg; p = peripatoid; f = foetus; a = adolescens I; ? = not known because not sampled during this period.

(c) Laboratory cultures of adolescens I

These cultures were started with 244 individuals, but there was considerable mortality so that this number declined, in an approximately exponential manner, to 6 individuals over the 20 weeks that we maintained the cultures. This was despite regular feeding, the absence of predators or external parasites, and the maintenance of a high humidity throughout. The declining numbers over time are shown in Table 3. Despite the problem of accumulating mortality, the experiment gave clear answers to

two of the three questions posed (see Methods); but the answer to the third remains elusive.

TABLE 3

THE DESIGN OF THE ADOLESCENS I CULTURING EXPERIMENT AND THE NUMBERS SURVIVING AT SELECTED TIME-POINTS

Sex	Temp.	No. of boxes[1]	Number of individuals[2]			
			Week 0	Week 6	Week 14	Week 20
Male	10°C	6	64	17	6	1
Male	17°C	6	61	16	8	2
Female	10°C	6	59	18	5	2
Female	17°C	6	60	17	7	1
TOTALS	-	24	244	68	26	6

1. The number of individuals per box at the outset was typically 10, but with a range of 9-13.
2. Survivorship is given for weeks 0, 6, 14, and 20, which are respectively the start of the experiment, the week when we first recorded weights, the last reliable data-set ($n \geq 5$ in all treatments), and the week in which the experiment was terminated.

No moult occurred in any of the 244 individuals up to either their death or the termination of the experiment at 20 weeks. Also, the number of coxal pores, which was checked at the beginning, in the middle and at the end of the experiment, was always one on each side. It is clear from this combination of observations that: (a) no 'cryptic moult' to a previously unrecognized stage occurs; and (b) the moult to adolescens II does not occur within 20 weeks, even with a constant temperature of 17°C, which is broadly equivalent to providing a continuation of summer conditions.

The question of whether any growth occurred without moults is harder to answer for two reasons. First, because although the three measures of size generally increased (Table 4), the increases were small; and second, because in batch culture with unmarked individuals it is impossible to distinguish between growth and selective

mortality, both of which would produce an increasing mean value over time. So, further experimental work with all individuals either marked or kept in separate containers will be necessary to resolve this issue.

TABLE 4

BODY SIZE MEASUREMENTS IN THE ADOLESCENS I CULTURES

(a) Head Width (mm)

Sex	Temperature	Week				Direction of change
		0		14		
		Mean	+/- SE	Mean	+/- SE	
Male	10°C	0.35	0.004	0.38	0.007	↑
Male	17°C	0.37	0.004	0.39	0.004	↑
Female	10°C	0.35	0.004	0.37	0.010	↑
Female	17°C	0.37	0.003	0.39	0.006	↑

(b) Body Length (mm)

Sex	Temperature	Week				Direction of change
		0		14		
		Mean	+/- SE	Mean	+/- SE	
Male	10°C	12.12	0.121	12.42	0.473	↑
Male	17°C	12.37	0.136	13.06	0.371	↑
Female	10°C	12.54	0.136	12.40	0.534	↓
Female	17°C	12.48	0.143	13.21	0.286	↑

(c) Weight (mg)

Sex	Temperature	Week				Direction of change
		6		14		
		Mean	+/- SE	Mean	+/- SE	
Male	10°C	1.45	0.043	1.47	0.084	↑
Male	17°C	1.44	0.070	1.73	0.092	↑
Female	10°C	1.22	0.035	1.58	0.132	↑
Female	17°C	1.52	0.058	1.77	0.094	↑

DISCUSSION

The sort of microhabitats in which broods were found at our study sites were broadly similar to those found by Lewis (1961) at Cuckmere Haven. However, our broods

were generally found closer to the high tide line than Lewis's. This feature is probably determined by the nature of the available habitat. At Whitburn, a very steep slope, in some places nearly vertical, is encountered only a metre or so after the strand line indicating the extent of the most recent spring high tide. At North Berwick and Brora the shingle gives way abruptly to grassy terrestrial habitat about 3m from the high tide line. None of our three sites had a shingle bank which it was possible for the animals to go behind, as was possible at Cuckmere. The distribution of brood sizes at Whitburn was generally in the lower half of the overall distribution (3-44 eggs) given by Lewis (1981). However, since Lewis's figures are for mature oocytes per female whereas ours are for eggs or young per brood, the two are not directly comparable, and the difference between them is probably explicable through the effects of 'perinatal' mortality.

The timing of egg-laying and hatching, and the progress through the early postembryonic stages to adolescens I at Whitburn was remarkably similar to that described by Lewis at Cuckmere, despite the difference in latitudes, as shown in Table 2. Our single samples from each of the two Scottish sites also corresponded with the Cuckmere and Whitburn timing pattern (Brora - all broods at the egg stage in late June; North Berwick - all broods at the Adolescens I stage in early August). However, without daily sampling at all localities over a 3-month period, which is hardly a practical proposition, small differences could go un-noticed. Økland (1984) states that in Norwegian populations (near Bergen), eggs are laid in late June, though he gives no data to support this statement. So perhaps there is a slight rather than nonexistent effect of latitude. Of course, it would help if we knew what environmental factor(s) induced egg-laying. We have tried to make *S. maritima* produce broods in the laboratory by varying temperature and photoperiod, both separately and together; but none of the combinations of conditions we have tried so far have worked.

It is interesting that our laboratory-reared adolescens I specimens did not moult to the adolescens II stage, especially in the case of those few that survived for 20 weeks at 17°C. It seems likely that in the field developmental processes will operate very slowly under the low-temperature conditions that typically prevail from October/November through to about March/April. So we might expect that although the adolescens I stage lasts from August to the following June in the wild (Lewis 1961), most of the internal changes necessary to enable the transition to adolescens II would occur in the period between about March and June. Our temperature of 17°C is clearly higher than the average that would occur in field habitats during that period, which approximately corresponds in timespan to the maximum period for which we kept individuals at 17°C (i.e. 20 weeks).

As will be clear from the above, there are still many gaps in our understanding of the reproductive and developmental biology of *S. maritima*. Nevertheless, it is clearly the best 'model system' species within the Geophilomorpha. Thus it is worth persevering; and there is no shortage of questions for future work on this system to address.

ACKNOWLEDGEMENTS

REFERENCES

Barber, A.D. and Keay, A.N. (1988) *Provisional Atlas of the Centipedes of the British Isles*. Biological Records Centre/NERC, Huntingdon.

Kettle, C., Johnstone, J., Jowett, T., Arthur, H. & Arthur, W. (2002) The pattern of segment formation, as revealed by *engrailed* expression, in a centipede with a variable number of segments. *Developmental Biology*, (in subm.)

Knight, C.G., Patel, M.N., Azevedo, R.B.R. & Leroi, A.M. (2002) A novel mode of ecdysozoan growth in *Caenorhabditis elegans*. *Evolution & Development*, **4**: 16-27.

Lewis, J.G.E. (1961) The life history and ecology of the littoral centipede *Strigamia (Scolioplanes) maritima* (Leach). *Proc. Zool. Soc. Lond.* **137**: 221-248.

Lewis, J.G.E. (1962) The ecology, distribution and taxonomy of the centipedes found on the shore in the Plymouth area. *J. Mar. Biol. Ass. U.K.*, **42**: 655-664.

Lewis, J.G.E. (1981) *The Biology of Centipedes*. Cambridge University Press, Cambridge.

Økland, S. (1984) Changes in heart ultrastructure during development of *Strigamia maritima* Leach (Myriapoda, Chilopoda, Geophilidae). *Int. J. Insect Morphol. & Embryol.* **13**: 233-245.