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Partial brood release in woodlice: A bet-hedging tactic?

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In many organisms, including woodlice, juvenile mortality is unpredictable, hence female behaviours that result in a temporal spread of reproductive output would be favoured by natural selection. Observations of brood release in several species of woodlice revealed that approximately 7% of females released between two and 10 young up to 24 h in advance of their siblings. Although under laboratory conditions offspring fitness measures between precocious young and their siblings were not significantly different, the tactic of partial brood release is considered as a risk avoidance or 'bet-hedging' female behaviour not previously recorded in this specialized group of Crustacea.

In baie organismes, insluitende houtluise, is die mortaliteit onder jong diere baie onvoorspelbaar. As gevolg hiervan, sal wyfies wat hulle reproduktiewe opbrengs temporeel kan versprei, 'n selektiewe voordeel geniet. Waarnemings op verskeie houtluisspesies het getoon dat ongeveer 7% van die wyfies tussen twee en 10 van hulle kleintjies vrystel tot soveel as 24 h voor die res van die broeisel. Alhoewel die oorlewingspotensiaal tussen die vroegvrygestelde kleintjies en hul sibbe nie onder laboratoriumtoestande betekenisvol verskil het nie, word gedeeltelike broeiselvrystelling as 'n risikovermydingstaktiek beskou. Sulke gedrag is nog nie voorheen in hierdie gespesialiseerde groep van die skaaldiere beskryf nie.

Any female in a population would be expected to adopt life-history tactics that will promote her reproductive success (e.g. Fisher 1930). Female behaviours that enhance offspring survival or reduce the variance in juvenile mortality would be favoured by selection, particularly if there is minimal energetic or survivorship cost. In many species females can partition current reproductive output into a temporal sequence of discrete partial clutches over the duration of the breeding season (Burley 1980; Clutton-Brock 1992). This is a common tactic when juvenile survival cannot be guaranteed by the female, for example where juvenile mortality factors are spatially or temporally unpredictable.

In woodlice syngamy is internal and fertilized eggs descend into a fluid-filled chamber, known as the brood pouch or marsupium, which consists of overlapping oostegites that are produced during a parturial moult. Embryonic development lasts for approximately 26 days at which time the cuticle has been secreted and the yolk supply exhausted. The young rupture the outer membrane of the egg capsule and escape into the brood pouch where they remain for several days during which time the marsupium fluid disappears (Sutton 1972). It is assumed that brood release occurs when the movement of the newly mobile offspring causes the oostegites to 'rupture' and the fully independent young are able to crawl out.

As part of a larger study on the reproductive biology of woodlice (see review by Dangerfield & Telford, in press a) gravid females near to brood release were isolated under controlled laboratory conditions in brood release chambers (Dangerfield & Telford 1990). These chambers were designed to provide conditions for the release of offspring and allow young to escape potential cannibalism by the mother. The chambers consisted of plastic pill boxes 5,0 cm in diameter × 1,6 cm deep covered with 1,5 mm diameter nylon mesh inverted into 6,5 cm diameter plastic beakers. The beakers contained moist plaster of Paris to a depth of 1,3 cm which maintained humidity conditions. Gravid females were placed in individual chambers when near to brood release and monitored at least once every 12 h.

Partial brood release was recorded in 14% of female *Porcellionides pruinosus* Brandt collected from a population in Gaborone Botswana. Two females sampled (7,4%) from a population of *Aphiloscia villis* Budde-Lund from Marondera, Zimbabwe also released seven (70% of total fertility) and four (30%) young in advance of their siblings. Observations of temperate species showed that partial brood release also happens occasionally in *Porcellio scaber* Latreille and in *Armadillidium vulgare* Latreille (4,3% of 114 observations). The phenomenon may not be frequent but appears to occur widely among different species.

In a population of *P. pruinosus* from Harare, Zimbabwe, 11 females (7,6% of females that produced broods in the chambers) released between two and 10 offspring, 8–24 h in advance of the remaining brood (Table 1). Offspring released in advance of their siblings amounted to around 30,9% of the total brood and occurred in females with a wide range of size (11,14–31,58 mg) and fertility (8–36 offspring).

The 'precocious' offspring were not significantly different in size to their siblings in three broods, significantly smaller in five broods and significantly larger in two broods (Table 1). Survivorship probabilities, based on culturing individual offspring in the laboratory (see Dangerfield & Telford, in press b), did not differ significantly between 'precocious' offspring and their siblings (paired t test, $t = 0,67$; $p > 0,1$; $n = 10$) and in two broods, where the numbers surviving allowed an assessment of growth rate, there were no significant differences in relative growth rate ($t = 0,28$ and 1,70;

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Table 1 Female mass (mg), fertility (F), proportion of brood released early (E), mean birth mass (mg) of first and second release offspring and p values of t test comparisons, for *Porcellionides pruinosus* from Harare, Zimbabwe

♀ mass (mg)	F	E	Mean birth mass (mg) 'first'	'second'	p value
15,9	25	20,0	0,289 ± 0,009	0,229 ± 0,003	**
31,6	36	11,1	0,171 ± 0,004	0,186 ± 0,003	*
11,3	14	21,4	0,184 ± 0,003	0,197 ± 0,007	ns
12,1	17	47,1	0,189 ± 0,004	0,223 ± 0,007	***
17,2	16	25,0	0,201 ± 0,010	0,247 ± 0,007	**
15,9	20	10,0	–	–	
21,3	33	36,4	0,185 ± 0,007	0,214 ± 0,002	**
15,2	11	36,4	0,219 ± 0,014	0,260 ± 0,015	ns
17,6	19	52,6	0,206 ± 0,003	0,215 ± 0,005	ns
13,8	17	17,7	0,241 ± 0,003	0,209 ± 0,003	***
11,1	8	62,5	0,167 ± 0,004	0,211 ± 0,005	**

$p < 0,05$; ** $p < 0,01$; *** $p < 0,001$; ns not significant.

$p > 0,1$ in both cases).

There are two possible positive fitness consequences of partial brood release. In natural environments, juvenile mortality is high, up to 90% of natality after four months (Hassall & Dangerfield 1990). There is also considerable spatial variation in this mortality, for example, as a consequence of predation (Sunderland & Sutton 1980). Temporal variation in the release of offspring is likely to separate siblings which could benefit the female through insurance against total brood loss. This would be an example of a risk avoidance behaviour that falls within the general concept of bet-hedging (Slatkin 1974). It would also be consistent with selection to avoid worst case conditions, in this instance total brood failure (Houston & McNamara 1992). It is also possible that, by delaying the release of part of the brood, those offspring that remain behind suffer reduced mortality. Immediately following release from the marsupium offspring undergo a series of moults. It is over this time period that offspring suffer the greatest mortality (Dangerfield & Telford, in press b); probably as a consequence of increased vulnerability to fluctuating environmental conditions. Those offspring that remain behind may begin the moulting process but because they are buffered against environmental change suffer less mortality than their previously released siblings. However, the limited data available suggest no significant influence of partial release on offspring survivorship.

Retaining part of the brood in the marsupium is a form of limited parental care by the female as it will delay the onset of the post-parturial moult necessary to initiate any subsequent reproductive events. However, as females store sperm (Sassaman 1978), there is no additional trade-off between a delay in offspring release and the timing of fertilization of the next brood. We would expect partial brood release to occur under field conditions as well as in the relatively benign laboratory conditions of this study. However, the occurrence of partial brood release under field conditions is difficult to establish and remains an interesting unexplored life-history tactic for females.

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