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## Schizamniogenesis in the rusty bat, *Pipistrellus rusticus*

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Rusty bats are seasonally monoestrous, carrying a single foetus in each of the two uterine horns. Implantation is superficial with amniogenesis initiated very early during embryogenesis. Contrary to most other bat species where the amnion is formed by folding, it is formed by cavitation in the rusty bat.

Roeskleurvlermuis is seisoenaal monestrus en dra 'n enkele fetus in elk van die twee uterushorings. Inplanting is oppervlakkig en amniogenese neem reeds baie vroeg 'n aanvang tydens embriogenese. In teenstelling met die meeste ander vlermuis-spesies waar die amnion deur vouing gevorm word, geskied dit in die roeskleurvlermuis deur middel van uitholling.

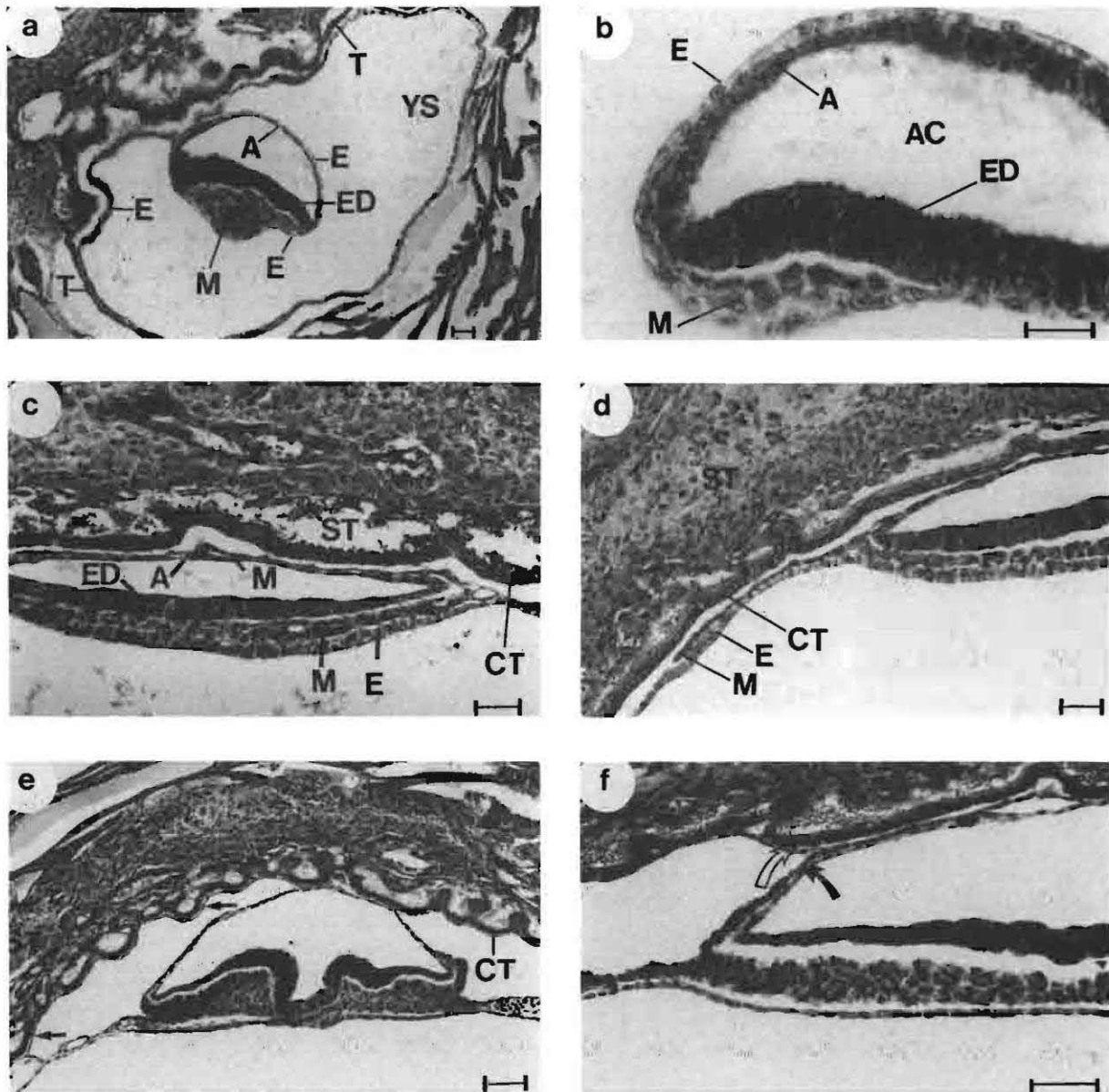
The rusty bat (*Pipistrellus rusticus*) is one of the smaller vespertilionids, with a body mass of between 3 and 4 g (Skinner & Smithers 1990). In the Southern African subregion it occurs in the northern and eastern Transvaal, Zimbabwe, northern Botswana and north-eastern and central Namibia (Meester, Rautenbach, Dippenaar & Baker 1986). Rusty bats are seasonally monoestrous giving birth to twins in November. The uterus is bicornuate, the uterine horns being of equal size and each carrying a single foetus during pregnancy (Van der Merwe & Rautenbach 1990).

Mossman (1937) recognized two distinct methods of amnion formation: formation by folding and formation by cavitation, with the latter being considered more specialized. He reported that the type of amniogenesis is correlated with the method of implantation so that the pleuramnion, which is formed by folding, is associated with superficial implantation and the schizamnion, formed by cavitation, with interstitial implantation.

Ten female rusty bats were collected during September 1988 in the Transvaal, 30 km NE of Vaalwater, South Africa (24°08'S; 28°18'E). All ten individuals were in early stages of pregnancy.

The genital tracts, complete with intact embryos were dissected out, fixed in Bouin's fluid, embedded in paraffin wax, serially sectioned (5 µm), mounted and stained with Ehrlich's haematoxylin and counterstained with eosin.

Implantation in the rusty bat was superficial, but the inner cell mass developed a cavity which persisted as the true or definitive amniotic cavity (Figure 1a). The roof of the amniotic cavity did not rupture at any stage and eventually formed the ectodermal part of the amnion (Figure 1a & b), while the floor of the amniotic cavity formed the embryonic disc (Figure 1a–c). The basal layer of the trophoblast (cytotrophoblast), underlying the syncytiotrophoblast (Figure 1c & d) formed the ectodermal component of the chorion throughout development. The inner surface of the chorion eventually became covered with extra-embryonic mesoderm.



**Figure 1a** Implanted embryo of the rusty bat, showing the ectodermal component of the amnion (A) formed during cavitation. The spherically shaped embryo is nearly completely enveloped by endoderm (E). Where the endoderm meets dorsally to the amnion, it does not fuse, but expands all along the inside of the trophoblast (T) to eventually form the yolk-sac (YS). At this stage the primitive streak has already started to form because mesoderm cells (M) are accumulating between the embryonic disc (ED) and the endoderm (E). Bar = 50  $\mu\text{m}$ . **1b** Higher magnification of the same embryo shown in 1a. This photograph of the embryo was taken adjacent to the point where the enveloping endoderm meets dorsally to the amnion before spreading sideways to line the trophoblast. Here it can be seen that, during the early stages of embryonic development, the spherical embryo is covered externally by endoderm (E). At some places the ectodermal component of the amnion (A) is more than one cell layer thick. The amniotic cavity (AC) still contains some debris. Mesoderm cells can be seen between the embryonic disc (ED) and the endoderm. Bar = 30  $\mu\text{m}$ . **1c** An older embryo where the embryonic disc (ED) has become flattened. As a result of this, the ectodermal component of the amnion (A), which is now completely covered externally by a layer of extra-embryonic mesoderm (M), has been stretched into a thin layer. Underneath the embryonic disc, the mesoderm (M) and endoderm layer (E) are visible. At this stage the cytotrophoblast (CT) underlying the syncytiotrophoblast (ST) is as yet not lined with mesoderm. Bar = 50  $\mu\text{m}$ . **1d** Embryo showing the extra-embryonic mesoderm (M) expanding between the endoderm (E) and cytotrophoblast (CT), underlying the syncytiotrophoblast (ST). Bar = 50  $\mu\text{m}$ . **1e** Embryo showing the extra-embryonic mesoderm (arrows) lining the cytotrophoblast (CT). Dorsal to the cytotrophoblast is the syncytiotrophoblast (ST). Bar = 50  $\mu\text{m}$ . **1f** Embryo showing the amnion (solid arrow) adjacent to the chorion (open arrow). Bar = 50  $\mu\text{m}$ .

It did not rupture at any stage and persisted over the entire embryonic hemisphere of the embryo (Figure 1a-d). With the flattening and expansion of the embryonic disc, the roof of the amniotic cavity (ectodermal part of the amnion)

became stretched into a thin layer (Figure 1a-f). Eventually this layer became covered externally by extra-embryonic mesoderm originating from the primitive streak (Figure 1a-c). As the true amnion was present from the beginning

(owing to cavitation of the inner cell mass), the floor of the amniotic cavity (embryonic disc) with overlying amnion maintained a spherical shape for some time. In the youngest implanting blastocyst of the present study, the spherically shaped embryonic disc and amnion, was almost completely enveloped externally by endoderm (Figure 1a & b). Where the endoderm met on the dorsal surface of the amnion, it did not fuse, but expanded outwards along the inner surface of the trophoblast to form the bilaminar yolk-sac (Figure 1a). As the embryonic disc unfolded (flattened out), the ectodermal part of the amnion became stretched into a thin layer but never ruptured. Owing to the flattening and expansion of the embryonic disc, the enveloping endoderm became straightened out underneath the embryonic disc and eventually adopted its characteristic appearance as a more or less parallel layer running underneath the embryonic disc (Figure 1c-f). The mesoderm, which had already started to appear during early embryonic development (Figure 1a & b), spread out between the embryonic disc and underlying endoderm. When the mesoderm reached the perimeter of the embryonic disc, entering the extra-embryonic space, it split into two layers. The upper layer of extra-embryonic mesoderm grew upwards, around the perimeter of the embryonic disc to cover the ectodermal layer of the amnion externally (Figure 1a-f). The lower layer of extra-embryonic mesoderm expanded further into the extra-embryonic region between the endoderm and overlying cytotrophoblast (Figure 1d). This lower layer of extra-embryonic mesoderm expanded as a single layer (Figure 1d), until it reached a point more or less corresponding with the perimeter of the syncytiotrophoblast (overlying the cytotrophoblast). From here, it appeared, the layer of extra-embryonic mesoderm turned and grew back along the inside of the cytotrophoblast until it united on the dorsal surface of the amnion (Figure 1d & f). In this manner the extra-embryonic mesoderm covering the amnion lay adjacent to the extra-embryonic mesoderm lining the cytotrophoblast (Figure 1f).

The phyllostomatids and desmodontids have been considered exceptional among bats in exhibiting complete interstitial implantation (Hamlett 1935; Wimsatt 1954). In members of both these groups amniogenesis, by means of cavitation, has been described e.g. *Glossophaga soricina* (Hamlett 1935; Rasweiler 1974) and the vampire bat *Desmodus rotundus* (Wimsatt 1954). In contrast, the cavitation of the inner cell mass shown by most other bat species serves only to form the primitive amniotic cavity which soon disappears. In these latter species cavitation does not contribute to the formation of the definitive amnion. In these instances the roof of the cavity or primitive amnion degenerates, and the definitive amnion is subsequently formed by a typical folding process (da Costa 1919, 1920; Gopalakrishna & Karim 1979, 1980; Mossman 1937; Wimsatt 1944). The rusty bat is unique in that although implantation is superficial, the amnion is formed by means of cavitation. A notable difference between the rusty bat and *G. soricina* is the extent to which the endoderm surrounds the inner cell mass. I support the opinion of Rasweiler (1974) that the precociously formed extraembryonic mesoderm dorsal and lateral to the inner cell mass, described by Hamlett (1935) for *G. soricina* and Wimsatt (1954) for *D. rotundus*, may be a mis-

interpretation, and that it is in fact endoderm. Unfortunately, owing to a lack of sufficient material preceding implantation and cavitation of the inner cell mass, the history of the endoderm enveloping the embryonic disc and amnion during the stages preceding implantation in the rusty bat is not certain. In the rusty bat it appears that the endoderm does not separate from the inner cell mass to envelop and suspend it from the cytotrophoblast, as is the case with *G. soricina* and apparently *Desmodus rotundus* (see Rasweiler 1974). Looking at Figure 1a and especially 1b of the present study, which is a much more advanced embryo compared to those described for *G. soricina* by Rasweiler (1974), it is clear that the endoderm forms a single smooth layer around the embryonic disc and amnion, with no apparent sign of becoming disorganized or degenerative along the surface of the amnion. It would rather appear that the endoderm delaminates from the embryonic disc and then expands around the amnion until meeting dorsally. From there it then expands along the inner surface of the trophoblast to form the bilaminar yolk-sac.

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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 reprodutiewe 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 broeisiel. 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  $\times$  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  $1,70$ ;