

## RESEARCH NOTE

### EXTENDED NEST RESIDENCE AND CANNIBALISM IN A JUMPING SPIDER (ARANEAE, SALTICIDAE)

**Keywords:** Sociality, parental care, matriphagy, sub-social

*Menemerus bracteatus* (L. Koch 1879) is a large unidentate Australian salticid that nests under the bark of eucalypt trees (Davies & Žabka 1989). During an earlier work (Rienks 1992) several nests were found on the scribbly gum, *Eucalyptus racemosa* Cavanilles. While studying the microhabitats of a wide range of salticid species, it was noted that sometimes a single nest of this species was occupied by numbers of large juveniles and the dead and shrunk body of a conspecific adult female, possibly the mother. It is common for juvenile salticids to remain with the mother for the first instar after emerging from the postembryo stage (Richman & Jackson 1992), but nest sharing by larger juveniles and an adult female is unusual. My observations suggested the juveniles of *M. bracteatus* may feed on their mother, a behavior known as matriphagy. Matriphagy, although known in a variety of spider families, has not been documented for salticids. In the present paper, I provide data on nest structure, nest residence and predators other than conspecifics. Also, I examine the hypothesis that juveniles of *M. bracteatus* cannibalize their siblings and practice matriphagy. Voucher specimens have been lodged with the Queensland Museum (QM S.47193).

Four study sites in forests in which the scribbly gum was common were selected in the Brisbane metropolitan area. Three sites were in Toohey Forest, Griffith University Campus; and one was in woodland adjacent to Tingalpa Reserve. In each site, I sampled the occupants of as many nests as possible. No nests were found in the first search which was made when the scribbly gums had just begun shedding bark (late October to early November). A search between late December and early January revealed 35 nests in various stages of construction, 24 of which contained

at least one clutch. A further seven nests found were from the previous season (evidence: constructed on older bark attached to the shedding bark, and contained shed exoskeletons only).

**Description of nests.**—Nests were constructed in the curve of the shedding bark and had tough roof and outer walls which strongly adhered to both the shedding bark and the tree trunk. Each nest had two reinforced entrances with projecting lip-like flaps above and below the entrance slit which may hinder access by predators and parasites. Nests were very strongly constructed and could be removed intact by carefully pulling the loose bark piece away from the tree trunk.

Most nests appeared to be in an early stage of construction. Of the 11 nests which contained no clutches, seven appeared to have been just begun and consisted of the outer walls only (three of these contained adult females), while the other four contained what appeared to be preyed-upon clutches (stained mass in which some individual chorions could be distinguished) and may have been abandoned. Counts were made of the number of clutches, and the number of eggs per clutch in each nest for 23 nests. A total of 54 clutches (median of two per nest) were found: 26% of the 23 nests contained one clutch, 30% contained two, 30% contained three and 13% contained four or more. Nests containing four or more clutches were completely filled with clutches and densely packed with loose sheets of very sticky silk laid down between successive clutches. In contrast, nests with fewer clutches were only partially filled with a conspicuous gap between the nest contents and the nest roof.

The number of eggs per clutch was between 9–45 (mean 23.8, SD 6.9,  $n = 32$ ) Eggs were

Table 1.—Stages found in previous season's nests of *Menemerus bracteatus*. Numbers marked with an asterisk are nests in which adult remains were found. Nest 1, which may have been from the 1995–6 season, had been subjected to substantial insect attack; and its contents were almost entirely gone, leaving the outer nest wall only. Remains of individuals that had apparently been preyed upon are indicated by the number found, followed by "p". Instar determination is based on size of the carapace of the shed exuviae.

Nest	Larva	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar
1	0	0	0	0	0	1	0
2*	19	25	32 + 1p	11 + 1p	0	0	0
3	27	26	35	22	0	0	1
4	27	25 + 2p	18	7	0	0	0
5*	35	19	24	18	4	1	0
6	36	36	26	29	2	0	0
7	26 + 1p	27 + 1p	26 + 1p	13	10	0	2

pale orange in color, did not adhere to each other, and were enclosed in a loose bag of non-sticky silk. Regardless of whether they were developing or apparently preyed-upon, clutches were included in calculations if the original numbers of eggs could be accurately determined. Numbers of eggs per clutch (clutch size) did not vary significantly with apparent order of laying (outermost clutch taken to be the most recent). Of the 23 nests in which clutches were examined in detail, the oldest stage of development included the egg (57% of nests), embryo (9%), prelarva (4%), larva (13%), first instar (13%) and second instar (4%) (terminology after Foelix (1996) which follows that of Vachon (1957)).

In total, 43% of the nests had one or more clutches showing signs of development. Three nests contained a clutch consisting of eggs, developing eggs, and prelarvae and/or larvae, suggesting that development of eggs within a clutch tends not to be synchronous. In two nests containing four or more clutches, clutch development showed a cohort effect with separation of cohorts by up to one instar (i.e., modal numbers at every second stage). One of these nests contained 2–3 clutches of eggs (total of 71 eggs), 31 larvae and 34 first instars. The second nest contained one clutch of eggs (25 eggs), 19 prelarvae, 7 larvae, 31 first instars and 5 second instars.

**Nest residence by juveniles.**—The seven nests collected that were from the previous (1996–7) season contained shed carapaces and exoskeletons of, in total, seven distinct stages, including the larval stage and six instars (Table 1). The largest carapace was considerably

smaller than adult-sized. The numbers of carapaces at each stage was more or less constant from the larval stage through to the third and sometimes the fourth instar (as shown by second and third instar carapaces). Numbers then declined rapidly, suggesting that dispersal had occurred in the third and fourth instars. If nests of this species usually contain about four clutches then it appears that the number of juveniles that survived to disperse as fourth (or occasionally third or fifth) instars, was equivalent to 1–1.5 full clutches. The presence of carapaces of large juveniles (fifth instar and older) suggested that juveniles may use the natal nest as a retreat for five or more instars.

**Cannibalism in the nest.**—Sometimes entire clutches, still enclosed in the silk bag, contained empty chorions, and had apparently been eaten. Such clutches were found in the nests from both seasons. Also, I found several apparently preyed-upon individuals (larvae and later stages) in three nests from the previous season (Table 1). Two of the current season's nests that contained four clutches and were more developed than the other nests were examined in more detail for signs of cannibalism. All first and later instars in both of these nests had grossly enlarged abdomens, consistent with having recently fed. All larvae had small abdomens which were similar in size to those of the prelarvae, suggesting that they had not fed.

It appears that more clutches are laid than survive to disperse (see above). Since the number of larval carapaces in the previous season's nests never exceeded 36 (the equivalent of just over one clutch), it is likely that

the older instars preyed upon prelarvae and larvae in addition to eggs.

Two nests from the previous season contained what were apparently adult remains, in one case the dorsal part of the carapace of an adult-sized individual, and in the other case, trachea attached to fragments of abdominal cuticle. It was not possible to determine whether these remains were those of adult females.

**Predation.**—Of the 23 nests collected in the 1997–8 season that were examined in detail, 26% contained one or two larvae of *Austromantispa imbecilla* (Gerstaecker) (Neuroptera: Mantispidae). The mantispid larvae from each of these nests, all of which initially contained either two or three clutches, were reared until pupation. In all cases, only a few eggs and larvae survived, the rest apparently being consumed by the mantispid. Four other nests contained clutches that had apparently been preyed upon by other predators. In total, 43% of 23 nests contained preyed-upon clutches with some nests having one (22% of nests), two (17%) or three (4%) clutches affected.

The young of *M. bracteatus* postpone dispersal from the natal nest until between the third and fifth instars, far later than is observed for most salticids. Another example of extended nest residence may also occur in *Hypaeus cucullatus* Simon 1900, because females and groups of juveniles of various sizes have been observed to share nests in this Central American salticid (Jackson 1989), but examples of juveniles cohabiting beyond the first and second instar are better known in maternal-social web-building spiders (Tretzel 1961, in Shear 1970; Kullmann 1972), and in spiders with more extended sociality (Jacson & Joseph 1973; Seibt & Wickler 1987; Evans et al. 1995).

In *M. bracteatus*, the extended nest residence, and the consequent large size attained by juveniles before dispersing, may be facilitated by the laying of multiple clutches in the same nest. This provides opportunity for juveniles to feed upon sibling eggs and probably also larvae and prelarvae. The finding of adult remains in old nests suggests that, as in many maternal-social (Bristowe 1958; Tretzel 1961, in Shear 1970; Kullmann 1972) and permanent social species from families other than the Salticidae (Jacson & Joseph 1973; Seibt

& Wickler 1987; Evans et al. 1995), matriphagy may occur in this salticid species. Perhaps the adaptive significance of the long duration of nest residence by juveniles may be primarily facilitation of matriphagy.

The laying of multiple clutches in the same nest probably does, however, have drawbacks. For other salticids comparable to *M. bracteatus* in size (females ranged from 9.5–11.5mm), the interval between oviposition of successive clutches tends to be 20–30 days. Assuming that the inter-clutch interval is comparable for *M. bracteatus* it is probable that a maternal female would need to make intermittent feeding forays away from the nest during the time span required for multiple oviposition. While at the nest, the female may be able to guard her eggs against the attacks of predators and parasites, but leaving the nest to feed would be likely to expose her broods to higher risks of attack by other spiders, ants, beetles and acrocerid flies and so forth (Austin 1985). The tough nest construction and complex, dense sticky silk packing of *M. bracteatus* nests may provide an exceptionally difficult barrier for enemies to penetrate when the maternal females is away (see Austin 1985), but the protection provided appears to be limited. The finding of preyed-upon clutches in many nests, including some in nests that appeared to have been abandoned early during construction, suggests that predation while the female is away may be significant. Nests of *M. bracteatus* were also vulnerable to attack by *A. imbecilla*, a mantispid and a specialist predator of spider eggs. Mantispid larvae consumed virtually all the eggs in the nests examined (see also Downes 1985) suggesting that maternal *M. bracteatus*, by laying all their clutches in the one nest, potentially place at risk their entire season's, and perhaps lifetime's, reproductive effort.

Females of *M. bracteatus* may lay all their clutches in one nest because overlying bark on scribbly gum trunks is both sparse and ephemeral, and so nest sites are in short supply. Theory suggests that egg cannibalism and delayed juvenile dispersal may arise because the oviposition sites of females are widely separated from the juvenile habitat (which may be the case in *M. bracteatus*) and that an unknown fitness advantage accrues to females by producing fewer, larger young (Crespi 1992). Alternatively, this delay, and the con-

sequent larger size of juveniles at dispersal, may be a fortuitous outcome of the opportunity to cannibalize siblings (and possibly, the mother) afforded by constraints on nesting sites.

Cannibalism of siblings in the nest is common in many solitary spider species (Krafft 1982) and it also occurs in some species with extended sociality (Evans et al 1995, but see Brach 1975). It has been argued that sociality in spiders evolved in some via an extension of an initial tolerant phase in the egg sac (Avilés 1997). The occurrence of sibling cannibalism in *M. bracteatus* is therefore interesting because it exists alongside a tolerance amongst larger juveniles.

Studies have shown that colonial-living web-building spiders capture more prey than solitary individuals, but that they are also subject to "costs" unique to this way of life, i.e., an increased vulnerability to predators and parasites as the size of the colony increases (see Uetz & Hieber 1997 and references therein). Most social spider species occur in the tropics (Avilés 1997) where numbers of specialist predators and parasitoids are very high (Begon et al. 1996). The occurrence in the solitary maternal social sub-tropical *M. bracteatus* of high rates of nest predation by a specialist mantispid egg predator raises the possibility that high rates of predation or parasitism could be a cause rather than simply a consequence of group-living in spiders.

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#### LITERATURE CITED

Austin, A.D. 1985. The function of spider egg sacs in relation to parasitoids and predators, with spe-

- cial reference to the Australian fauna. *J. Nat. Hist.*, 19:359–376.
- Avilés, L. 1997. Causes and consequences of cooperation and permanent sociality in spiders. Pp. 476–498, *In* The Evolution of Social Behaviour in Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.). Cambridge Univ. Press, Cambridge.
- Begon, M., J.L. Harper, & C.R. Townsend. 1996. *Ecology. Individuals, Populations and Communities*. 3rd ed. Blackwell Scient. Publ., Boston, Oxford.
- Bristowe, W.S. 1958. *The World of Spiders*. Collins, London.
- Brach, V. 1975. The biology of the social spider *Anelosimus eximius* (Araneae: Theridiidae). *Bull. Southern California Acad. Sci.*, 74:37–41.
- Crespi, B.J. 1992. Cannibalism and trophic eggs in subsocial and eusocial insects. Pp. 176–213, *In* Cannibalism. Ecology and Evolution among Diverse Taxa. (M.A. Elgar & B.J. Crespi, eds). Oxford Univ. Press, Oxford.
- Davies, V.T. & M. Žabka. 1989. Illustrated keys to the general of jumping spiders (Araneae: Salticidae) in Australia. *Mem. Queensland Mus.*, 27(2):189–266.
- Downes, M.F. 1985. Emergence of *Austromantispa imbecilla* (Gerstaecker) (Neuroptera: Mantispidae) from the retreat web of *Mopsus pencillatus* (Araneae: Salticidae). *Australian Entomol. Mag.* 12(3):54.
- Evans, T.A., E.J. Wallis & M.A. Elgar. 1995. Making a meal of mother. *Nature*, 376:299.
- Foelix, R.F. 1996. *The Biology of Spiders*. 2nd ed. Oxford Univ. Press, New York, Oxford.
- Jackson, R.R. 1989. An unusual nest built by *Hypaeus cucullatus*, a jumping spider (Araneae, Salticidae) from Costa Rica. *Bull. British Arachnol. Soc.*, 8(1):30–32.
- Jacson, C.C. & K.J. Joseph. 1973. Life history, biometrics and behaviour of the social spider *Stegodyphus sarsinorum* Karsch. *Insectes Sociaux*, 20(2):189–204.
- Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communication: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton Univ. Press, Princeton, New Jersey.
- Kullmann, E.J. 1972. Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). *American Zool.*, 12:419–426.
- Richman, D. & R.R. Jackson. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). *Bull. British Arachnol. Soc.*, 9:33–37.
- Rienks, J.H. 1992. Influences of microhabitat structure on the colour patterns of jumping spiders (Araneae: Salticidae). Ph.D. Thesis, Griffith University, Brisbane, Australia.
- Seibt, U. & W. Wickler. 1987. Gerontophagy ver-

- sus cannibalism in the social spiders *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock. *Anim. Behav.*, 35(6):1903–1904.
- Shear, W.A. 1970. The evolution of social phenomena in spiders. *Bull. British Arachnol. Soc.*, 1(5): 65–76.
- Uetz, G.W. & C.S. Hieber. 1997. Colonial web-building spiders: Balancing the costs and benefits of group-living. Pp. 458–474, *In* The Evolution of Social Behaviour in Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.). Cambridge Univ. Press, Cambridge.
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