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Notes on nesting behaviour in *Bembix bubalus* Handlirsch in southern Africa with the emphasis on nest sharing and reaction to nest parasites (Hymenoptera: Sphecidae)

by

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ABSTRACT

Data on the nesting behaviour of *Bembix bubalus* Handlirsch are presented. Of particular note is an instance of nest sharing as this appears to be the first record of nest sharing by a progressive provisioner in the Sphecidae. An instance is recorded of a wasp provisioning, in addition to its own larva, the larvae of a sarcophagid fly which had parasitised the nest.

INTRODUCTION

Due to the current interest both in nest sharing and in response to parasitism it seems useful to publish this account of the nesting of *Bembix bubalus* despite its preliminary nature, particularly as opportunities for such studies are not as common in southern Africa as might be supposed.

The present paper is based on a preliminary investigation of three days duration carried out during a short visit to the Oudtshoorn district in December 1986. A follow up investigation was planned for January 1987 but due to unforeseen problems a second visit to the area in the summer of 1986/1987 did not come about. The site was revisited in December 1987, that is in the following summer. Unfortunately, whereas there had been a thousand or more individuals of *Bembix bubalus* nesting there, when the preliminary observations were made, there were then fewer than a dozen wasps attempting unsuccessfully to excavate nests. The sand had become so destructured, due to drought and trampling, that their efforts were in vain. This decline in nesting activity was particularly disappointing as, in the course of their investigations of the nesting of wasps in the arid areas of southern Africa during the past two decades, the authors had not previously found any species of *Bembix* nesting in aggregations of more than about a dozen. Nesting aggregations of several hundred (Evans, 1957) or thousand (Bequaert, 1932) have, however, been reported for some species of *Bembix* elsewhere in the world.

THE NESTING OF *BEMBIX BUBALUS* HANDLIRSCH

Description of the nesting area

The nesting aggregation covered an area, approximately 300 m^2, of level friable sandy soil

Fig. 1. Nesting area of *Bembix bubalus* Handlirsch at Onverwacht, Oudtshoorn district.

sparsely vegetated. The site lies on the flood plain of the Kammanassie River at Onverwacht (33° 37′ 35″S, 22° 14′ 18″E) to the south of Oudtshoorn in the Little Karoo.

This area situated immediately inland of the Outeniqua Mountains lies in a rain shadow and consequently receives an annual rainfall of only 240 mm. Rain may fall during any season of the year, however, spring and late summer are the wettest periods. The soils above the flood plain are relatively coarse grained and are of the Cretaceous Enon Formation. Those of the flood plain on which the nesting site of *B. bubalus* is situated are light coloured, finer textured and are of diverse provenance having been carried down from further east by the river. The area lies within Acocks' Veld Type 26, False Karroid Broken Veld (Acocks, 1953, 1975 and 1988). The area is characterized by dwarf scrub, with a noticeable succulent element, and with taller shrubs mainly along the water courses (Fig. 1).

Nest excavation and temporary closure

The nests were excavated in the usual *Bembix* manner: that is the two fore-legs, equipped with sand rakes, were repeatedly swept back in unison whilst the abdomen was synchronously raised and lowered allowing the soil to be shot out behind the wasp.

The spoils of excavation were drawn back to some little distance from the nest entrance where they accumulated to form a tumulus up to 65 mm in diameter. Throughout nest excavation and provisioning the tumulus was not dispersed by the wasp.

Fig. 2. Female *Bembix bubalus* Handlirsch in flight carrying her prey, a bombyliid fly, held ventral side up close beneath her.

Nests were temporarily sealed with sand when wasps were away from them and when wasps were within them but not actively working, for example in cloudy weather or at night.

During nest excavation miltogrammine flies were observed stationed on perches, such as nearby twigs, in close proximity to nests. From their behaviour it was clear that they were monitoring the wasps' nesting activities.

Male behaviour

Males were common in the nesting area during the period of the investigation 10–12.xii.86 when nesting by a thousand or more females was in full swing. They were seen to fly rapidly low over the ground frequently changing direction and patrolling the entire area of the nesting aggregation.

At the time of the second visit to the study site on 8.xii.87 when there were fewer than a dozen females attempting to nest only one male was observed. This male was actively interested in all the females. Each time he spotted a female he advanced towards her with a markedly high pitched buzzing flight, came above her and tapped her with his abdomen. Only one female was seen to accept his advances, that is to permit him to grasp her and to fly off with her. Actual copulation was not observed.

Identity of the prey, carriage of the prey and satellite flies

Seventy eight prey were obtained, 24 from females captured flying with prey and 54 from nests (Table 1). The latter category was made up of complete prey and prey in the form of recognizable remnants. All prey were flies, the vast majority (91%) being flower-visiting flies of the families Bombyliidae and Syrphidae, suggesting that *B. bubalus* seeks prey at flowers.

Although actual prey capture was not witnessed large numbers of wasps were observed flying with prey. In many instances these wasps were accompanied by satellite flies. The prey fly is held ventral side up, close beneath the wasp by her middle-pair of legs when she is in flight (Fig. 2). On nearing her nest the wasp moves the fly back (Fig. 3) so that her approach to the nest is very "tail heavy". She alights at the concealed nest entrance and immediately clears the sand with her fore-legs whilst standing on her hind-legs (Fig. 4) and continuing to hold the prey with her middle-legs. Opening of the nest and entry into it are rapid so that little opportunity is given to the satellite flies for larviposition.

Of interest was the observation of a female which due to some disturbance dropped her prey, a large syrphid, and without hesitation returned, dived down and picked up her prey without alighting.

Description of twelve nests, the nature of their contents and a record of the presence of three wasps in a nest

A sample of twelve nests was excavated. Nine of these were unicellular and of a typical basic

Fig. 3. A female *Bembix bubalus* Handlirsch in flight carrying her prey, a syrphid fly (*Eristalinus taeniops* (Wied.)), and preparing to land.

TABLE 1.

Prey of *Bembix bubalus* Handlirsch taken with wasps in flight and from the nests excavated at Onverwacht, Oudtshoorn district, 9–12 .xii.86.

Identity of prey	no. taken with wasp in flight	no. taken from nest										no.total
		1	2	3	4	5	6	7	8	9	10	
?STRATIOMYIDAE												
?Genus and species	—	—	—	—	—	—	—	—	1	—	—	1
TABANIDAE												
Chrysops obliquifasciata Macquart	—	—	—	—	—	—	—	—	—	1	—	1
BOMBYLIIDAE												
Bombylius discoideus F.	1	—	—	—	—	—	—	—	—	—	—	1
Bombylius ornatus Wied.	2	—	—	1	—	—	—	—	—	1	—	4
Bombylius ?sp.	—	—	2	—	—	—	—	1	—	—	—	3
Exoprosopa sp. A	—	1	—	—	1	—	1	—	—	—	—	3
Exoprosopa sp. B	—	—	—	—	—	—	1	—	—	—	—	1
?Exoprosopa	—	1	—	—	—	4	—	—	—	1	—	6
Systoechus sp. A	5	—	1	1	1	5	2	—	—	—	—	15
Systoechus sp. B	1	—	9	—	—	—	—	—	—	—	—	10
Villa sp. A	—	—	—	—	—	—	—	—	—	—	1	1
Villa sp. B	2	—	—	—	—	—	—	—	—	—	—	2
?Genus and species A	—	1	—	—	—	—	—	—	—	—	—	1
?Genus and species B	—	—	—	—	—	1	—	—	—	—	—	1
												48
SYRPHIDAE												
Allograpta calopus Wied.	—	—	—	1	—	—	—	—	—	—	—	1
Eristalinus taeniops (Wied.)	5	8	—	—	1	1	—	—	—	—	—	15
Eristalis tenax (L.)	5	—	—	—	—	—	—	—	—	—	—	5
?Genus and species A	—	—	—	—	1	—	—	—	—	—	—	1
?Genus and species B	—	—	—	—	1	—	—	—	—	—	—	1
												23
MUSCIDAE												
Musca sp.	1	—	—	—	—	—	—	—	—	—	—	1
SARCOPHAGIDAE												
?Genus and species	—	—	—	—	—	—	1	—	—	—	—	1
TACHINIDAE												
?Genus and species A	—	1	—	—	—	—	—	—	—	—	—	1
?Genus and species B	1	—	—	—	—	—	—	—	—	—	—	1
?Genus and species C	1	—	—	—	—	—	—	—	—	—	—	1
												3

Fig. 4. A female *Bembix bubalus* Handlirsch holding her prey, a syrphid fly (*Eristalinus taeniops* (Wied.)), with her middle-legs whilst standing on her hind-legs and opening her nest with her fore-legs.

Bembix nest pattern (Evans, 1957 and Gess, 1986), that is, with a short sloping entrance burrow dipping down to end in a spur and giving rise just above the spur to a secondary shaft ending in a large ovoid cell (Fig. 5). Of the three remaining nests one was two-celled, one three-celled and the third four-celled (Fig. 6). Shaft diameter was 9–9,5 mm, cell diameter 12,5–14 mm and cell depth 130–170 mm.

Six of the unicellular nests each contained a wasp larva with one or two prey flies and fly fragments. Two were empty. The ninth contained a wasp larva, three large sarcophagid maggots, two small sarcophagid maggots, eleven partially eaten prey flies and fly remains.

Only one cell in each of the two-celled nests and in the three-celled nest contained a wasp larva and prey flies.

In the four-celled nest two of the cells contained cocoons and fly remains, the third a large wasp larva and fly remains, and the fourth a small wasp larva, fly remains and a freshly introduced prey fly. One female had been observed taking a fly into the nest and a female, presumed to be this female, had been captured when she was leaving the nest. The nest upon excavation was found to contain two additional females. Each was positioned facing outwards within a cell containing a feeding larva which she appeared to be guarding.

It is noteworthy not only that three females should have been present in the nest but that, that being so, there were only two wasp larvae being actively provisioned.

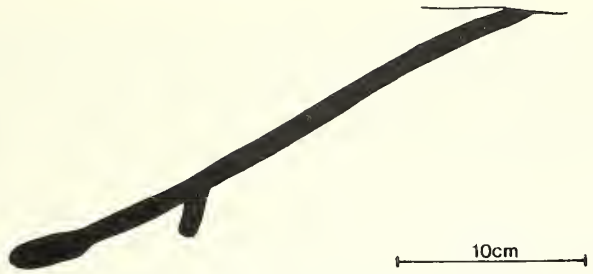

Fig. 5. Plan of a unicellular nest of *Bembix bubalus* Handlirsch investigated at Onverwacht, Outshoorn district, 10–12.xii.86

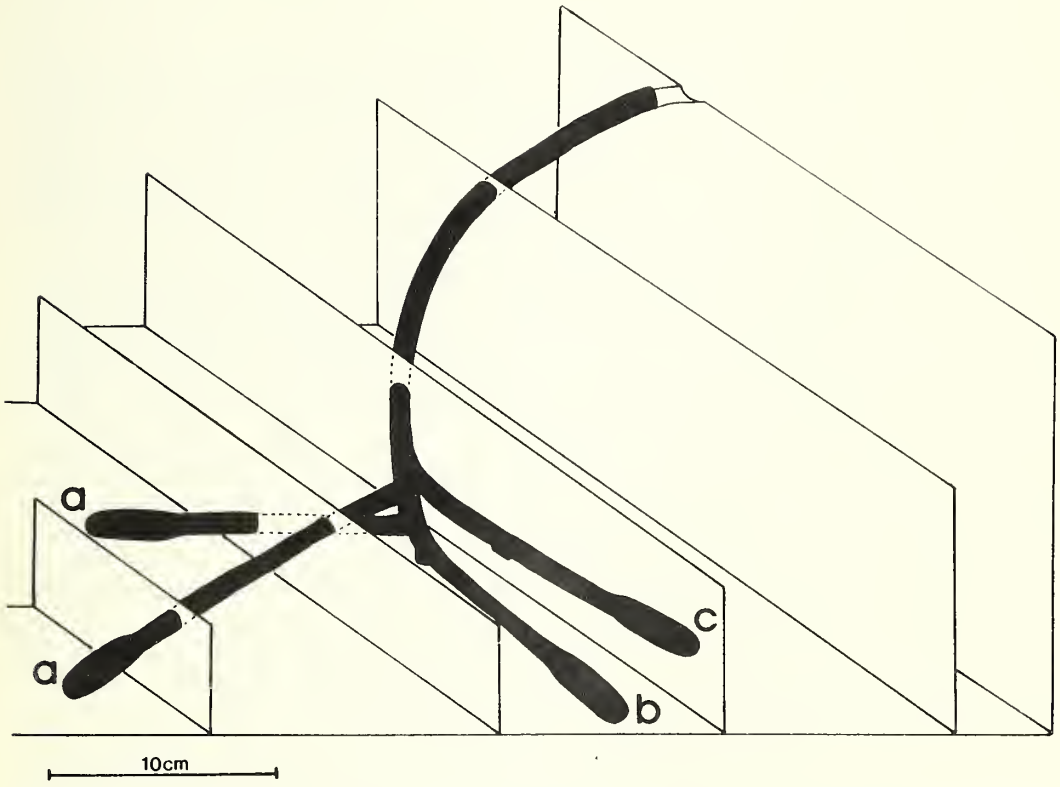

Fig. 6. Plan of the four-celled nest of *Bembix bubalus* Handlirsch investigated at Onverwacht, Oudtshoorn district, 10–12.xii.86: **a**–cell containing wasp-cocoon and fly remains; **b**–cell containing large wasp-larva and fly remains; **c**–cell containing small wasp-larva, entire fly and fly remains.

Visits to nests by more than one female

It was observed that in several instances nests were being visited by more than one female. Furthermore when two females had entered a nest neither was evicted. During the short period of the study, three days, during which provisioning of nests was being actively pursued no case of two or more females taking prey into a nest was noted. It is therefore not known whether any one nest was being provisioned by more than one female.

Provisioning mode

In common with the majority of species of *Bembix, B. bubalus* is clearly a progressive provisioner, that is the larva is provided with fresh prey throughout its development.

Voltinism

B. bubalus is clearly bi-voltine or multivoltine as an adult emerged before the end of the 86/87 summer season from a cocoon obtained from one of the cells of the four-celled nest.

DISCUSSION

It seems of interest to consider whether the findings for *B. bubalus* are of any particular significance in a consideration of the ethology of Sphecidae and of solitary aculeate wasps as a whole.

The points to be considered are: the variation in the number of cells; the presence of three wasps in one of the nests in relation to the development of presocial behaviour; and the wasp's reaction to the presence of sarcophagid maggots in her nest.

The variation in the number of cells in itself is not of particular note. Tsuneki (1956), in Japan found that, though the nest of *Bembix niponica* F. Smith is typically unicellular, in some nesting aggregations about 4% of the nests were compound and in one exceptional aggregation the majority of nests contained two or more cells. Further, observations on *Bembix nubilipennis* Cresson in North America (Evans, 1966) suggest that that species when bi-voltine may make multi-cellular nests in spring and unicellular nests in autumn.

What is, however, of note is that the four-celled nest of *B. bubalus* was occupied by three wasps. It would appear therefore that *B. bubalus* practises facultative nest sharing. The nearest recorded approach to this condition in *Bembix* seems to be the observation by Evans (1966), in North America, that in *Bembix amoena* Handlirsch nesting aggregations, where nests are in very close proximity, one nest entrance may serve more than one nest. However, in that species the burrows diverge immediately beneath the ground surface so that there is only entrance sharing, not nest sharing as exhibited by *B. bubalus*.

Observations that two wasps could enter a nest without either being evicted and that one nest was found to be occupied by three wasps is indicative of a breakdown in territoriality, which is a pre-condition to nest sharing and co-operative behaviour.

Relatively few studies of Sphecidae provide evidence of co-operative behaviour. An interesting example of differential aggression is exhibited by the mass provisioning nyssonine *Sphecius speciosus* Drury (Pfennig and Reeve, 1989) which tolerates the intrusion of large near neighbours into the nest but only when no prey cicada is exposed. Examples of actual nest sharing have been recorded for species in the sub-families Sphecinae (Brockmann and Dawkins, 1979; Brockmann, Grafen and Dawkins, 1979; Eberhard, 1972 in Evans, 1977), Pemphredon-

inae (Matthews, 1968 in Evans, 1977), Crabroninae (Bowden, 1964; and Evans, 1964 and Peters, 1973 both in Bohart and Menke, 1976) and Philanthinae (Alcock, 1975; Evans, 1973; Evans and Hook, 1982a, 1982b, and 1986; Hook, 1987). All are for mass provisioners, that is all the provision required for the development of the larva is generally provided before the hatching of the egg. The present record for *B. bubalus* is therefore probably the first for nest sharing by a nyssonine and is also probably the first example of nest-sharing by a progressive provisioner to be recorded for the Sphecidae. That *B. bubalus* is a progressive provisioner is of particular interest as it therefore exhibits a combination of para-social behaviour, that is adult females of the same generation associate in a common nest, and sub-social behaviour, that is the larvae are cared for by a parent for some time after hatching. This behaviour combination has otherwise, for wasps, been recorded only in the Vespoidea. Furthermore as *B. bubalus* is at least bi-voltine the possibility exists that wasps of two generations may come into contact in a nest.

At this point it is of interest to consider the accounts of Alcock (1975), Evans and Hook (1982a, 1982b and 1986) and Hook (1987) of nest sharing by some species of *Cerceris* (Philanthinae). Some evidence was obtained of differentiation in the roles of the females associated with the nest. Some appeared to be provisioners and others non-provisioners. Females of both types showed mandibular wear, suggesting that both were involved in preparing cells, also both types had ovaries containing well-formed oocytes, which suggested that both laid eggs more or less regularly. Non-provisioners were considered to perform an important function as guards but no suggestion was made as to what factors determine whether a female is a provisioner or not.

The fact that in the four-celled *B. bubalus* nest three females were present but only two cells were being provisioned and that both of these were being guarded leads one to ask whether there is here too some degree of division of labour or co-operation between the females.

Finally it is of interest to consider the response by *B. bubalus* to nest parasites. It has been suggested that gregarious nesting may be a "selfish herd" response to parasites and Wcislo (1984) sees parasites as important agents of selection for the maintenance of aggregations and thus for more advanced social levels as well. Evans and Hook (1986) in their study of *Cerceris* were satisfied that there is little doubt of the importance of guards in protecting the nest contents from invasion by ants and mutillids. On the other hand they found that flies which operate at the nest entrance are not deterred by guards, in fact, the delay sometimes caused by the guard to a prey-laden wasp entering the nest actually enhanced the attack by satellite flies which larviposit on the prey at the nest entrance. As *Cerceris* is a mass provisioner the introduction of fly maggots into the cell results not only in the consumption of the available prey but also of the wasp larva. *Sphex decipiens* Kohl (Sphecinae), the nesting of which was studied in the Grahamstown district by Gess and Gess (unpublished field notes, 1985/1986), which is a mass provisioner suffers a high incidence of loss of provision and larvae to the ravages of fly maggots. Evans (1966) suggested that in the case of progressive provisioners the fly maggots would most probably be detected and destroyed, and goes as far as to say that in the genus *Bembix* progressive provisioning has led to parasitism by miltogrammine flies being reduced to virtually zero (Evans, 1977).

This might well be the case in species which clean out their nests. The presence of fly remains in cells of *B. bubalus* containing cocoons indicates that this species does not clean out its cells. It was therefore of interest to discover its reaction to the presence of fly maggots in its cells. One single-celled nest was found to have been so parasitised. The cell which was still being actively provisioned contained a large wasp larva, three large fly maggots and two small fly

maggots. The wasp had not as one might have expected destroyed the fly maggots or abandoned the nest but was provisioning the maggots as well as her own larva. In doing so the wasp undoubtedly saved her larva from destruction by the maggots, however, she had succeeded in rearing only one wasp offspring when she might have reared several had she not been provisioning the maggots. Had she been a mass provisioner her energies would not have been wasted in this way. This seems a curiously disadvantageous result of what would otherwise appear to be an advanced behaviour pattern.

Clearly investigation of many more nests is required before any more definite statements can be made concerning: the incidence of nest sharing: the nature of and degree of co-operation between wasps sharing a nest: and the incidence of and response to nest parasitism.

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