Preliminary description of the predatory and nesting behaviour of *Tachypompilus analis* (Pompilidae: Pompilinae) in Hong Kong, China.

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ABSTRACT

Field observations of the hunting and nesting behaviour of *Tachypompilus analis* (Fabricius, 1781) (Pompilinae: Pompilini) were carried out by the author in the vicinity of his house in Hong Kong over several years. Behaviour on one particular nesting niche is described as well as the capture of a rare prey species.

It was noted that although the species is known to excavate shallow depressions in soil as nesting sites, *T. analis* also chooses pre-existing cavities in masonry. Additionally, *T. analis* was observed to prey upon a web-fabricating spider (Agelenidae or Amaurobiidae), a clear departure from the usual wandering type preyed upon by the genus. This choice affects the normal hunting sequences possessed by the genus. From fragmentary observations I suggest that *T.analis* may have some level of behavioural plasticity, probably providing a net gain in parental investment.

Key words: *Tachypompilus analis*; Pompilinae, Heteropodidae, Spassaridae, Lycosidae, Amaurobiidae, nesting sites.

INTRODUCTION

The Spider wasp *Tachypompilus analis* is a common representative of the Pompilidae (spider wasps) locally. This paper reports on the prey usage and hunting techniques of this pompilid, based on observations made by the author, over several years in his garden at Pak Sha O, Sai Kung, South East New Territories.

The Pompilidae is a cosmopolitan family comprising over 5,000 species in more than 230 genera worldwide (Pitts et al. 2005). All members are predatory, with the greater diversity occurring in the tropics. The family inner relationships have long been debated and several classifications have been proposed since the beginning of the 20th century. The latest cladistic analysis proposed by Pitts et al. (2005) recognises four subfamilies: Ceropalinae, Pepsinae, Ctenocerinae and Pompilinae. Pepsinae and Pompilinae make up the vast majority of the species in the family, with well over 2,000 species each. There have been only fragmentary and regional revisions of members of this family and considerable generic synonymy remains a problem (Pitts, 2005).

All members of the family prey upon spiders for larval food and invariably store the nest with one single paralysed prey item. There are only fragmentary records on the biology of members of the subfamily Pompilinae, but in all cases there seems to be a great variability of prey choice, with some species restricting themselves to a few members in one family, while others may use a wide range of prey in various families (Evans, 1953; Iwata, 1976; Wasbauer & Kimsey, 1985; O'Neill 2001; Pitts, 2005). Members of the genus *Tachypompilus* (Ashmead, 1902) are reported to be specialist predators of Lycosidae (wolf spiders) and the related families Pisauridae (fishing spiders) and Agelenidae (funnel web spiders) in the USA (Evans, 1953, Evans & Yoshimoto, 1962; Kurczewski & Kurczewski, 1968, 1973; Kurczewski, 1981, 1999; Wasbauer & Kimsey, 1985), although some also prey upon Heteropodidae (Huntsman Spiders) (Nakao & Iwata, 1964; Martins, 1991; O'Neill, 2001), and this is clearly a prey of choice for *T. analis* in Hong Kong.

Members of these spider families can be generally characterised as wanderers, without a permanent home, although most Agelenidae construct burrows with a silken finish. I report here on the observation in the field of the capture of a probable member of the Agelenidae or Amaurobiidae (lace-webbed spiders), families that build complex tangled webs terminating in a cavity where the spider lays in wait – necessitating a hunting strategy clearly in departure from that applied when hunting the normal wandering type of spiders. I also report on the intra-specific theft of prey.

Nesting habits of the Pompilidae range from leaving the prey *in-situ* after oviposition (ectoparasitoid), to dragging it into a pre-existing cavity before oviposition and, for the most "evolved", flying with dismembered prey and placing them in multi-cellular nests constructed wholly of foreign materials (mud) (Evans & West Eberhard, 1970; Iwata, 1976; O'Neill, 2001). Females of the genus *Tachypompilus* are known to drag paralysed prey backwards by the chelicerae or pedipalps to a dry spot, and excavate a shallow depression - by raking the soil with the front tarsi - into which the prey is deposited. An egg is laid on the abdomen of the prey and the depression is filled with the excavated soil and bits of debris, leaving no apparent traces of the nesting site (Evans & Yoshimoto, 1962; Wasbauer & Kimsey, 1985). I report here on the use of pre-existing cavities/crevices that the wasp may re-arrange as nesting sites.

Aculeate wasps are commonly compared to one another by using parental behavioural traits arranged on a increasing scale of behavioural complexity, culminating with the eusocial species (Table 1)), a model thought to represent the trend of evolution in wasps. Pompilids have been placed on the lower levels of this scale (Level 1, 2, 3, 4a & 4b of Table 1), because no representatives are known to have departed from the habit of provisioning one prey per egg and many construct a nest after prey capture, both characteristics thought to preclude gradual provisioning seen as necessary step towards brood care and social interactions (Evans, 1953; Evans & West Eberhard, 1970; O'Neill, 2001). Additionally, only a few species are known to nest gregariously (Evans & West Eberhard, 1970) or to have generational overlap on the same nesting site (O'Neill, 2001; Barthélémy and Pitts, in preparation), none of which are in the subfamily Pompilinae.

There are relatively few species of *Tachypompilus* worldwide but they are widely distributed, occurring in the Ethiopian, Oriental, Nearctic and Neotropical regions. *Tachypompilus analis* is the only reported species in the genus locally. It is widespread from the Nansei islands in Japan to Taiwan, the Philippines, Hawaii, South-East Asia and South Asia. It is a medium large wasp, wholly black save for the last four metasomal segments (in females; last five in males) which are bright orange/red. Locally, females measure 16-21mm, while males are markedly smaller measuring approximately 11mm. These dimensions seem to be larger for females than those measured in Taiwan by Tsuneki (1989), where it was found that females measured 13-15 mm, while in the Philippines female specimens were even smaller at 12-14mm. Female individuals from the Nansei Islands (Japan) range from 15 to 20mm (Yamane et al,1999).

Adults are known to feed on floral secretions and may also feed on the haemolymph oozing from the sting wound of the prey. Larvae are fed locally with at least three species of spiders in three distinct families:

- Sparassidae; *Olios* sp. (Figure1)
- Heteropodidae; Undetermined sp.1. (Fig.2).
- Agelenidae or Amaurobiidae; Undetermined sp. 2.

Additionally, in Japan the species is reported to prey on *Heteropoda venatoria* Linnaeus (Heteropodidae) (Nakao and Iwata, 1964), a species that also occurs in Hong Kong (Hills, 1981).

The Pompilids *Xanthampulex* sp. and *Irenangelus luzonensis* (Rohwer) (Ceropalinae) are reported to be cleptoparasites of *T. analis* (Williams, 1919; O'Neill, 2001). Tachinid flies are noted to attack the paralysed spider and consume it (Williams, 1919), and it may be possible that the spider wasp's prey also is consumed by scuttle flies (Phoridae) or satellite flies (Anthomyiidae).

MATERIALS & METHODS

Casual observations of the wasps were made over several years in various spots around the author's house and garden, Pak Sha O, Sai Kung Country Park, Hong Kong (UTM: 50Q KK 242 849, 70m asl). One niche has been used consistently over the years and is situated in the crevices of a north-facing stone wall behind a rain-water drainpipe, access to which is approximately 120cm off the ground. The actual nesting site was hidden from view. Observations at this site are summarised below.

On 12 May 2008, at around 15:00h, I witnessed in a disused "greenhouse" in my garden the attack and capture of a spider, nest construction and closure over a period of approximately one hour; events also described below.

Prey transportation was documented photographically in many instances and some examples presented in the Plate section.

The activity period of the *T. analis* was monitored by a resident Malaise trap, set between 2001 and 2009 in the authors garden along with casual sightings.

OBSERVATIONS

A busy niche behind a rain- water drainpipe

Over the past years this site has been occupied by successive generations of *T. analis*, from spring well into autumn, the wasps seemingly able to find various prey (Sparassidae and Heteropodidae) in the close vicinity. Invariably the wasps were seen walking backwards while dragging the prey by the pedipalps, and when they reached a point close to the foot of the wall near the drainpipe they would let go of the prey, walk around with much antennation, inspect the prey and often fly off, to check the nesting site and fly back shortly after. The wasps would grab the paralysed spider by the pedipalps and start the vertical climb to the nesting site.

The ascension was never an easy affair and the trajectory was oblique, sinuous and somewhat indirect. On occasion (in fact relatively often) the wasps would accidentally drop the load, obliging them to start the climb all over again. They were all extremely persistent and prey were never abandoned.

When the wasp left her prey for nest inspection, the abandoned item sometimes attracted other *T. analis* dwelling in the vicinity who would attempt to steal it, presumably for their own use, as observed on 2 July 2006. However, on that day the rightful owner came back before the theft was consumed, found its prey and the thief and engaged her in a violent fight where much biting and apparently stinging attempts occurred (Fig.3). The original owner was able to repel the other wasp and both individuals seemed to be unscathed by the fight. The winner groomed and resumed dragging the prey to the nest shortly afterwards.

At regular intervals during the season this nesting site becomes the scene of frantic activity when numerous males are seen patrolling the close vicinity of the niche, presumably to attempt mating with newly emerged females. However (and unfortunately), no mating was ever observed.

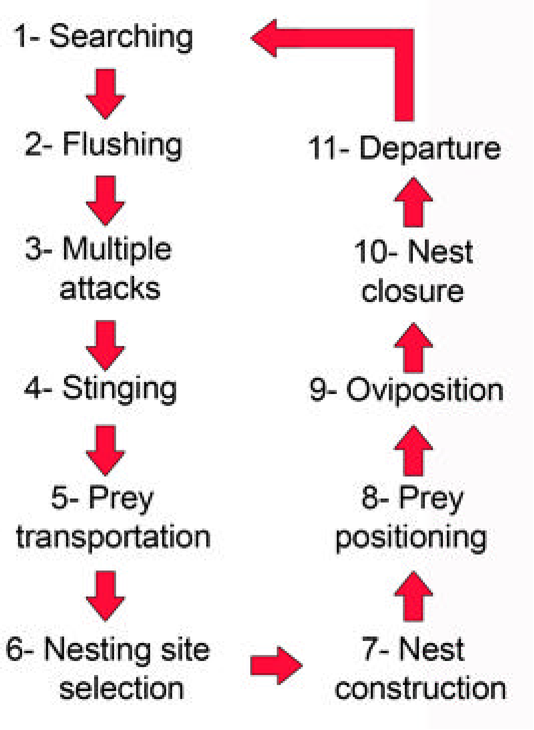
An unusual prey

A disused greenhouse was the site of a prolonged observation of prey capture, nest construction and closure. The soil was a dry mix of sand, clay and organic matter (disused vegetable patch). I was originally looking at the complex web that a spider had extended from the hollow end of a horizontal structural bamboo segment approximately 2 cm in diameter and 100cm off the ground. Numerous strands of silk had been spun from the bamboo to various elements of the greenhouse, forming an extremely tangled structure more or less conical extending horizontally for approximately 30cm and about 20cm at its maximum diameter. The webbing close to the bamboo was denser and formed a sheath or a funnel that extended into the hollow segment. The spider was laying in wait at the entrance of the bamboo cavity. From the architecture of this web I have tentatively identified the spider as belonging to either the Agelenidae or Amaurobiidae.

A *T. analis* wasp was seen shortly before landing on the web close to the entrance funnel. The flight seemed direct and the strands of silk did not stop the wasp. Upon landing she immediately penetrated the cavity without hesitation. This caused the spider to be flushed out with the wasp in pursuit. A small fight ensued, but the spider was faster on its web and managed to elude the wasp, and came to a halt on a strand of its web, while the wasp flew off. However, the wasp did not give up and circled the web again attacking the spider as soon as spotted, which prompted the spider to change position. It was obvious that the tangles of silk strands hindered the access to the spider, which managed to evade seven or eight attacks. However, under the constant harassment of the wasp, the spider eventually committed the fatal mistake of dropping to the ground, where she was immediately followed by the wasp. There, a very short pursuit ensued which resulted in the prompt paralysis of the spider. Unfortunately the sting location was not established. The spider was not much larger than the wasp.

As could be expected, the wasp used her mandibles to seize the spider by the pedipalps and drag it, walking backward for approximately 60cm, before dropping the prey. The wasp inspected a small patch of ground of approximately 40cm x 20cm, settling for one spot where she started to dig a cavity. However, she soon abandoned that position to begin at a new location, and in total, four sites were investigated before finally choosing one of them. Buttressed on her hind legs, she raked the soil very rapidly with her front tarsi, ejecting fine material under her body up to 10cm from the working area. Coarser bits and large items were seized by the mandibles and carried away. After approximately 40mins of digging – creating a conical cavity of approx 3.5cm in diameter and 1.5cm deep – the wasp stopped and started to compact the bottom of the cavity with rapid motions of the abdominal tip, doing so for less than two minutes. She walked to her prey, seized it and dragged it into the cavity, depositing it venter down, legs folded. Adjustments to the cavity were made for about five minutes and she continued to dig around and underneath the prey on one side then on the other, displacing the arachnid by using her abdomen as a leaver, cautiously placing the spider in the right spot. Oviposition was made ventrally on the prey but I cannot ascertain its exact position or the moment it happened. Covering up the prey took about 15mins, using the previously ejected soil but also new material. Finally, the area was compacted with the abdominal tip and there was no visible trace of the nesting site.

This behavioural sequence can be summarised as follows:



Sequence 2 and 3 could be grouped together under “Multiple attacks” and behaviours may contain sub-sequences, such as “Deposit prey” in sequence 5 and“Compacting” in sequence 7 and 10.

All through this observation, I saw a small fly hovering or resting at the proximity of the working site. *Tachypompilus analis* aggressively gave chase to this apparently passive fly when spotted, but the intruder would always reappear.

Discussion

The selection of nesting sites by the females and the choice of prey seem worthy of discussion.

Nesting sites

Using the evolutionary scale (Table 1) and the published literature (O'Neill, 2001) the genus *Tachypompilus* (and, in particular, *T. analis*) would be placed in Stage 3 by building a shallow depression. However, as described in this paper it often uses pre-existing cavities (possibly slightly modified), which would also place the species in Stage 2. It appears that *T. analis* may have a certain level of behavioural plasticity in its nesting patterns, excluding it from a clear classification on this evolutionary scale. The opportunistic use of variable nesting sites may in fact represent a net advantage in terms of parental investment and in this case offers more time to prepare more cells, increasing reproductive success although it has to be noted that the choice of an elevated nesting site rendered transportation difficult and on many occasions the prey was dropped, the wasp spending extra time and effort to deposit the item in the nest.

The descriptions by Williams (1919) and Iwata (1939) of the nesting behaviour of *T. analis* match the description above. Iwata (1939) also noted that the wasp would use both dry soil and crevices in walls. On the other hand, detailed descriptions of the nesting behaviour in the genus *Tachypompilus* by Strandtmann (1953) and Martins (1991) for *T.ferrugineus burrus* (Cresson) and *T. xanthopterus* Rohwer respectively – both New World species – show substantial differences. In both cases, the spider was placed venter up in the cavity and the wasp would manoeuvre herself underneath the prey to oviposit on the dorsal side, behaviour that is greatly different to what is described here, although other elements of behaviour such as carriage (5), site selection (6), cell construction (7) and cell closure (10) were essentially the same.

Prey

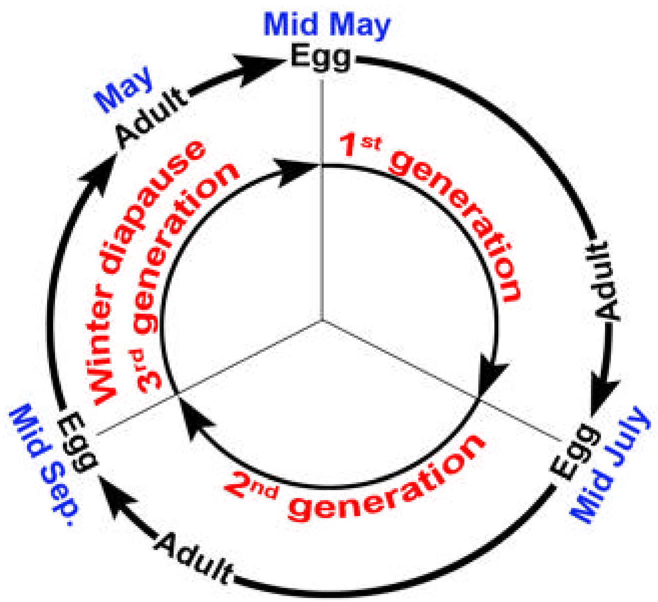
In the same way, prey choice in *T. analis* may show a level of flexibility that adapts it to various niches. Indeed, according to the literature the genus uses wandering spiders and is even considered a specialist hunter (Evans, 1953; Evans & Yoshimoto, 1962; Kurczewski & Kurczewski, 1968, 1973; Kurczewski, 1981, 1999; Wasbauer & Kimsey, 1985). The observation reported here of the predation on a web fabricating spider clearly departs from the known hunting habits, the wasp performing a particular initial set of behaviours ("1.search-2.flushing-3.multiple attacks-4.stinging") in conditions vastly different from those on the ground, a sequence that is more complex than the normal pattern of "1.search-2.pursuit-3.stinging" applied when hunting wandering spiders (Heteropodidae, Spassaridae, Lycosidae and Pisauridae).

Other members of the Pompilinae such as *Sericopompilus apicalis* (Say) or *Anoplius "marginatus"* (Say) are known to be predisposed to some level of variability in prey choice and hunting techniques (Kurczewski & Kurczewski, 1973; Kurczewski, 1981), but none have been described as "specialists". The possible plasticity of the hunting behavioural patterns may be the result of an adaptation to prey availability, although none of the normal prey are rare in the study area.

Voltinism

Assuming a development stage (from egg to adult) of approximately 45 days, we can infer that the species is at least bivoltine in Hong Kong and likely has three generations per year with the last one overwintering either as a diapausing larva, or a pupa. Additionally, it is very unlikely that any adult female would survive more than two months, meaning the active females sighted between July and October were not 1st generation individuals.

The activity period can be expressed by the following diagram:



CONCLUSION

While it is commonly accepted that complex behaviours evolve from simpler ones and are somewhat more adaptive, the example of *T. analis* perhaps shows that simple behaviours could also evolve from complex behaviours, depending on the situation. Could it be that our model of behavioural evolution remains an oversimplification of what evolution really is and that perhaps eusociality does not represent the most adaptive solution or the ultimate goal of evolution in wasps? However, the apparent plasticity of behavioural patterns in *T. analis* and in the genus generally may offer a rewarding research topic, to fully understand if these modifications are inherited behavioural traits or the result of experience. Further ethological studies in the sub-family/tribe and genus will be required in order to obtain sufficient series from which patterns can be extracted with confidence.

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Figure 1 (left). *T. analis* dragging a paralysed Sparassidae, *Olios* sp. (Photo author).

Figure 2 (below). *T. analis* dragging a paralysed Heteropodidae up a wall. (Photo author).

Figure 3 (below). A violent fight between two individuals of *T. analis*, the consequence of a prey theft attempt (Photo author).

Table 1. Sequences of parental behaviours in the solitary aculeate wasps. From O'Neill, 2001. Text in bold indicates the actual sequence of behaviours.

Stage	Provisioning Sequence	Occurrence
1	Parasitoid that leaves prey in situ: **Prey-egg**.	Ancestral condition of Aculeata, occurs in all Drynidae, all non-cleptoparasitic Chrysididae and Mutillidae, most Bethylidae, Thipiidae, Scoliidae and some Pompilidae and Sphecidae
2	Parasitoid that drags prey to a nearby niche that is sometimes modified: **Prey-niche-egg**.	Some Bethylidae, Tiphiidae, Scoliidae, Pompilidae and Sphecidae.
3	Single prey in a single-celled nest built *after* hunting: **Prey-nest-egg-nest closure**.	Most Pompilidae and a few Sphecidae.
4	Single prey in a nest built *before* hunting:	
4.A	Single-celled nest: **Nest-prey-egg-nest closure**.	Pompilidae, Sphecidae.
4.B	Multi-cellular nest: **Nest-prey-egg-cell-nest closure**.	Pompilidae
5	Mass provisioning:	
5.A	Single-celled nest: **Nest-prey-egg-more prey-nest closure**.	Sphecidae
5.B	Multi-cellular nest (egg laid on first prey): **Nest-(prey-egg-more prey-cell closure)-(multiple cells in same nest)-nest closure**.	Sphecidae
5.C	Multi-cellular nest (egg laid on last prey): **Nest-(many prey-egg-prey-cell closure)-(multiple cells in same nest)-nest closure**.	Common in Sphecidae and Crabronidae.
6	Progressive provisioning (egg laid after 1st prey brought in):	
6.A	Single-celled nest: **Nest-(prey-egg-more prey over several days)-nest closure**.	A few Sphecidae and Crabronidae
6.B	Multi-cellular nest: **Nest-(prey-egg-more prey over several days)-(multiple cells)-nest closure**.	Some Crabronidae, some Eumeninae
6.C	Several single-celled nests provisioned progressively at the same time.	Some Ammophilinae.
7	Mass or progressive provisioning (egg laid in empty cell before provisioning)	
7.A	Progressively provisioned single cell nest: **Nest-(egg-many prey over several days)-nest closure**.	A few Crabronidae
7.B	Mass-provisioned multi-cellular nest: **Nest-(egg-many prey [or pollen mass]-cell closure)-(multiple cells)-nest closure**.	Most Eumeninae, all Masarinae.
7.C	Progressively provisioned multi-cellular nest: **Nest-(egg-many prey over several days-cell closure)-(multiple cells)-nest closure**.	Some Eumeninae.