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COMPARATIVE BIOLOGY OF CAVE-DWELLING SPITTING SPIDERS (ARANEAE: SCYTODIDAE): PARENTAL CARE, COOPERATIVE PREY-CAPTURE, CANNIBALISM, NATAL DISPERSAL AND REPRODUCTIVE BEHAVIOUR

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***ABSTRACT*. –** Caves are among the most fascinating environments on Earth. Specialised cave biota provides evidence of evolutionary adaptations for living under severe conditions. However, little attention has been paid to the behaviour of cave spiders. In this study, we compared life history, including maternal care, cooperative prey-capture, tolerance among siblings, and reproductive behaviour, of five cave spitting spiders (Scytodidae). *Scytodes magna* and Guangxi *Scyloxes* sp. 1 occur exclusively in the aphotic zone, whereas *Scytodes fusca*, *S. cavernarum* and the Philippines *Scytodes* sp. 2 are usually found relatively close to cave entrances, known as the light zone. Like in other typical spitting spiders, females of *S. fusca*, *S. cavernarum* and the Philippines *Scytodes* sp. 2 carry their egg-sacs with their chelicerae. However, here we document for the first time that *S. magna* and Guangxi *Scyloxes* sp. 1 females do not carry their egg-sacs in their chelicerae. We found that, instead, they hang their egg-sacs on their webs, which is for the first time documented in scytodids. Although *S. fusca* is a widespread species that inhabits a wide range of habitats, we document for the first time that this species also lives in caves. The five species we studied can each be characterised as being non-social, but we found a few traits that deviate from the typical solitary characteristics. These include late natal dispersal in Guangxi *Scyloxes* sp. 1 spiderlings and low fecundity in *S. cavernarum*. We discuss possible explanations for the solitary habits adopted by the species we studied.

***KEY WORDS*. –** Spitting spiders, solitary, maternal care, cave.

INTRODUCTION

The specialised underground biota found in caves provide evidence of evolutionary adaptations for life under severe conditions that include reduction or absence of light, constant (usually very high) humidity, extremely stable temperature, high carbon-dioxide and low oxygen levels, and severely limited energy (food) input (Culver, 1982; Howarth, 1983, 1993; Parzefall, 1985; Culver & Sket, 2000; Culver et al., 2003). The energy input to caves is also low and usually allochthonous as there are no primary producers. In spite of these challenges, many animals live in cave environments, with invertebrates being especially common. Cavernicolous environments select for loss of characters that are unnecessary and costly to produce or maintain (e.g. eyes, pigmentation, thickened cuticle), and accentuation of characters that assist in resource location or compensate for the unnecessary characters lost (e.g. attenuated appendages, reduced metabolic rate) (Prendini et al., 2010). Cavernicolous environments also create natural barriers, limiting dispersal, restricting gene flow, and resulting in the evolution of localised endemics (Crouau-Roy, 1989; Lamoreaux, 2004).

Depending on the extent of physiological, behavioural and morphological specialisation, various cave ecomorphotypes can be recognised (Howarth, 1983, 1993). Obligate cavernicoles or troglobites are restricted to deep cave environments and are highly stenotopic. They exhibit pronounced troglomorphies, ecomorphological adaptations to hypogean habitats, including the loss or reduction of eyes and pigmentation. Troglobites include various species of blind Crustacea, Collembola and Pseudoscorpiones (Levy, 2007). There are a few species of troglobitic arachnids, some of which include the eyeless scorpion, *Akrav israchanani*, from the Ayyalon caves in Israel (Levy, 2007), the Mexican cave-dwelling harvestman, *Hoplobunus boneti* (Mitchell, 1971), and *Islandiana* sp. (Linyphiidae) of Florida caves (Peck, 1970). Facultative cave-dwellers or troglophiles are found in all cave habitats, from the entrance to the deep zone, and show intermediate degrees of adaptation to caves. Trogloxenes are species that utilise caves for shelter during the day but feed outside at night, and there are the cave accidentals as well (Barr, 1967).

Sociality in cave arthropods is rare. Having analysed what was known about cave ants, Wilson (1962) hypothesized that social insects "never become truly troglobitic" because "they are unable to maintain sufficiently large cave demes". It is implicit that the underlying reason is food scarcity. However, this view was challenged by the discovery of the first truly troglobitic ant, *Leptogenys khammouanensis*, from the caves of Laos. Voids of Laos, by providing large reservoirs of food, may have created an unusual opportunity for such evolution to occur (Roncin & Deharveng, 2003).

Many arachnids live in caves. Previous work on cave arachnids include studies of reproductive behaviour (e.g. Doran et al., 2001), analysis of adaptations to the hypogean environments (e.g. Hadley et al., 1981), examination of population genetic structures and speciation mechanisms (e.g. Hedin, 1997), and research on systematics and evolution (e.g. Arnedo, 2007), but little is known about the social behaviour of spiders and other arachnids that live in caves. Parental care has been documented in a neotropical cavernicolous harvestman, *Goniosoma longipes* (Machado & Oliveira, 1998; Machado et al., 2000). *G. longipes* females lay their eggs on the cave walls and guard their eggs for about two months, after which juveniles, having reached the first instar, disperse. Defense against egg dehydration, fungal attack, cannibalism and interspecific predation have been proposed to be important selective pressures for the evolution of parental care in cave *G. longipes* (Machado & Oliveira, 1998). Observations on the natural history of the newly described cave spider, *Goeldia zyngierae* (Titanoecidae), show that the interconnected webs contain 2–30 spiders of different life stages, living together. Almeida-Silva et al. (2009) thus suggested the possibility of subsocial behaviour in this species. However, this species is not exclusively cavernicolous (i.e., it is found in the surrounding epigeic region as well). Also, individuals of this species were not observed to feed together. However, when the web is disturbed, a group of spiders can be seen to move quickly towards the disturbed area. *G. zyngierae* may be a colonial spider, formed via the parasocial route. What this means is that individuals of this species, whether related or not, aggregate (for colonies), with the presence of a common resource (e.g., food) being an important factor favouring aggregation (Lubin & Bilde, 2007).

Drymusid spiders (Drymusidae), which are considered to be close to the spitting spider family Scytodidae (Labarque & Ramírez, 2007), are sometimes found in caves. Drymusid females usually rest on the underside of the web and also lay their eggs there (Labarque & Ramírez, 2007). Females of *D. dinora* Valerio and *D. spectata* Alayón García usually build white, spherical, wrinkled egg-sacs, which are occasionally hung in the web, close to them. They also carry their egg-sacs from place to place (Valerio, 1974; Alayón García, 1981), but they sometimes leave the egg-sacs to attack a prey in response to a web perturbation (Valerio, 1974). Nevertheless, there have been no detailed investigations of how drysmusid spiders care for their eggs and spiderlings. Scytodids have a prey-capture method that is unique for spiders. They spit on their prey, with the sticky substance expelled from their fangs gumming down the prey long enough for the scytodid to finish the attack by injecting venom (Foelix, 1996). Sociality is another unusual characteristic found among some species in the family Scytodidae. For example, *Scytodes fusca* in Australia appears to have a complex social structure that includes web sharing and prey capture (Bowden & Jackson, 1988). *S. intricata* from Panama (Eberhard, 1986) and *Scytodes* sp. from the Philippines (Li et al., 1999) show extended maternal care of eggs and young. Other scytodids that have been studied are solitary (Valerio, 1981; Eberhard, 1986; Li et al., 1999).

Seeing that the expression of sociality varies considerably in the Scytodidae suggests that we might find species in this family representing transitional stages in the evolution of sociality. This in turn suggests that scytodids present an exceptional opportunity to investigate the evolution of sociality. Because the study of scytodid social behaviour has literally just begun, the biology and behaviour of many taxa are not yet known in sufficient detail to answer many basic questions about these spiders. In addition, the evolution of sociality in this family should be amenable to testing by comparative analysis of social behaviour. Comparative information about scytodids in other species of the genus *Scytodes* and in other genera is thus particularly important. However, only seven species from a single genus *Scytodes* have been subjected to detailed behavioural studies and our knowledge of the presence of sociality in the remaining species and the degree of maternal care in the closest species or sister species of social species in the family Scytodidae is lacking.

Cave-dwelling spiders are of particular interest and currently four scytodid species are known from cave environments: *Scytodes eleonorae* from Brazil (Rheims & Brescovit, 2001), *S. cavernarum* and *S. magna* from Malaysia (Bristowe, 1952; Roewer, 1960), and *Stedocys uenorum* from Thailand (Ono, 1995). The only previous work on cave *Scytodes* includes the description of parental care of *S. eleonorae* from Goiás, Brazil that is known to live in caves at distance of up to 800 m from the cave entrance (Rheims &Brescovit, 2001). Like other non-cave *Scytodes*, females carry egg-sacs with their chelicerae. Detailed behavioural studies are lacking in *S. eleonorae* and other cave scytodids.

Table 1. Locality and the microhabitats of the five cave scytodids sampled from the field.

Species	Locality	Coordinates	Habitat type
Scytodes fusca	Malaysia: Batu caves, Selangor	N03°13'60 E101°42'0 93 m asl	Crevices of cave walls, mostly at cave entrance
Scytodes cavernarum	Malaysia: Gua Angin, Gunung Senyum, Pahang	N03°43'0 E102°25'60 57 m asl	Crevices of cave walls, ranging from cave entrance to few metres from entrance
Philippines *Scytodes* sp. 2	Philippines: Biak-na-bato National park, Luzon	N15°5'60 E121°4'0 196 m asl	Crevices of cave walls, inside cool windy areas of cave ranging from cave entrance to few metres from entrance
Scytodes magna	Malaysia: Batu caves, Selangor	N03°13'60 E101°42'0 93 m asl	Under loose rocks; deep crevices on cave walls, in the dark zone of cave, ranging from 100 m to 800 m from cave entrance
Guangxi *Scyloxes* sp. 1	China: Xi'an caves, Fengshan county, Guangxi	N24°33.941' E107°02.465 574 m asl	Ceiling of dark zone of caves, ranging from 50 m to 1 km from cave entrance

In this study, we aimed to determine the forms of sociality adopted by cave-dwelling scytodids. Five species were studied, with special attention to maternal care of egg-sacs, extended maternal care (food provisioning), group prey-capture, delayed dispersal, tolerance, fecundity, number of clutches, interval between clutches, and interval between hatching and egg-sac production. The five species are represented by two different genera: *Scytodes* and *Scyloxes*. The genus *Scytodes* includes *S. cavernarum*, *S. fusca* and *S. magna* from Malaysia, and *Scytodes* sp. 2 from the Philippines. The genus *Scyloxes* is represented by *Scyloxes* sp. 1 from Guangxi, China. If sociality exists in the cave scytodids, we ask the question whether it conforms to the *Goniosoma* model of gregariousness arising from defensive behaviour, or to that of *Goeldia* in which spiders aggregate around a common food resource, (i.e., sociality evolving from a parasocial precursor). If sociality arose from maternal care accompanied by an elaboration of the maternal care phase, this would be the first record of social cave spiders evolving via a subsocial precursor.

MATERIAL AND METHODS

Colony survey in the field

The scytodids (Fig. 1) were found in a variety of locations in caves (Table 1). *Scytodes magna* and Guangxi *Scyloxes* sp. 1 were found deep inside the caves where there was little or no light. Spiders were either hidden under large rocks or in holes carved deep into the cave walls. Many individuals of Guangxi *Scyloxes* sp. 1 constructed their webs on the ceilings of the caves. *Scytodes magna* and Guangxi *Scyloxes* sp. 1 showed an accentuation of the appendages such as legs and palps, and thinning of the cuticle. We classified these two scytodid species as troglobites on the basis of their morphology and on how they were found in the deep dark zones of the caves. *S. cavernarum* and the Philippines *Scytodes* sp. 2 were found mostly at the cave entrance or within 10–40 m of the entrance. A few individuals were also found at the edges of the dark zone (also known as the twilight zone). The difference was that the caves which were occupied by *S. magna* and Guangxi *Scyloxes* sp. 1 were largely undisturbed and in darkness whereas the caves of *S. cavernarum* and the Philippines *Scytodes* sp. 2 were opened to the public and hence had lightings installed inside the caves. *S. cavernarum* and the Philippines *Scytodes* sp. 2 were found in tight crevices along the cave walls, usually with a mass of silk and moss or debris covering the entrance of the crevices. *S. fusca* was found both at the cave entrance and inside the cave but within 20 m of the entrance. *S. fusca* is a widespread species. For example, we found this species in abandoned buildings, between wooden panels of kampong houses and inside water pipes. Bowden (1991) studied the intraspecific interactions of *S. fusca* that constructed web complexes in trees, and found them to be communal territorial in this habitat. In this study, we investigated whether cave-dwelling *S. fusca* (Table 1) displayed similar intraspecific behaviour to the tree-dwelling species described by Bowden (1991).

For simplicity, we adopted a convention used before (Li et al., 1999; Yap & Li, 2009) of referring to all webs occupied by scytodids as 'colonies'. We conducted a one-week survey in each of the respective locations to study the social structure of each cave spitting spider species. At 1-m intervals, all spiders and their webs were photographed and their activity (if any) recorded (e.g. feeding on prey, copulating or foraging), after which they were hand-collected. The following data was recorded: size and composition of the colony members (if any); the instar and gender of individuals; developmental stage of the colony (juveniles, females with egg-sacs). We also identified any prey items being attacked or eaten. Colonies were sampled once during the survey at each site. The life stages of juveniles were noted as first, second or later instars, with reference taken from the sizes of laboratory-cultured spiders of known instars. Data collected from the field were augmented with laboratory observations (see following sections).

Criteria used in determining the social status

Spider collection and maintenance. – For laboratory observations, spiders were collected from study sites and maintained by adopting protocol similar to that used in earlier scytodid studies (Li et al., 1999; Li, 2002; Yap & Li, 2009). Only the essential details are given here. All spiders were housed in a laboratory under controlled environmental conditions (temperature = 24 ± 1°C; relative humidity = 70–90%; light/dark cycle = 12 L : 12 D; lights on at 0800 h). They were fed with fruit flies, *Drosophila melanogaster* Meigen, once a week. Captive individuals were kept in plastic, cylindrical cages (diameter × height = 6 × 8 cm). Holes permitted the insertion of prey without damaging webs, and water was continuously available from moist cotton inserted through other holes or from glass vials filled with water, stoppered with cotton, and placed in the cages.

Life stages were referred to as, for example, egg, first instar (see Whitcomb, 1978). 'Penultimate instars' are one moult

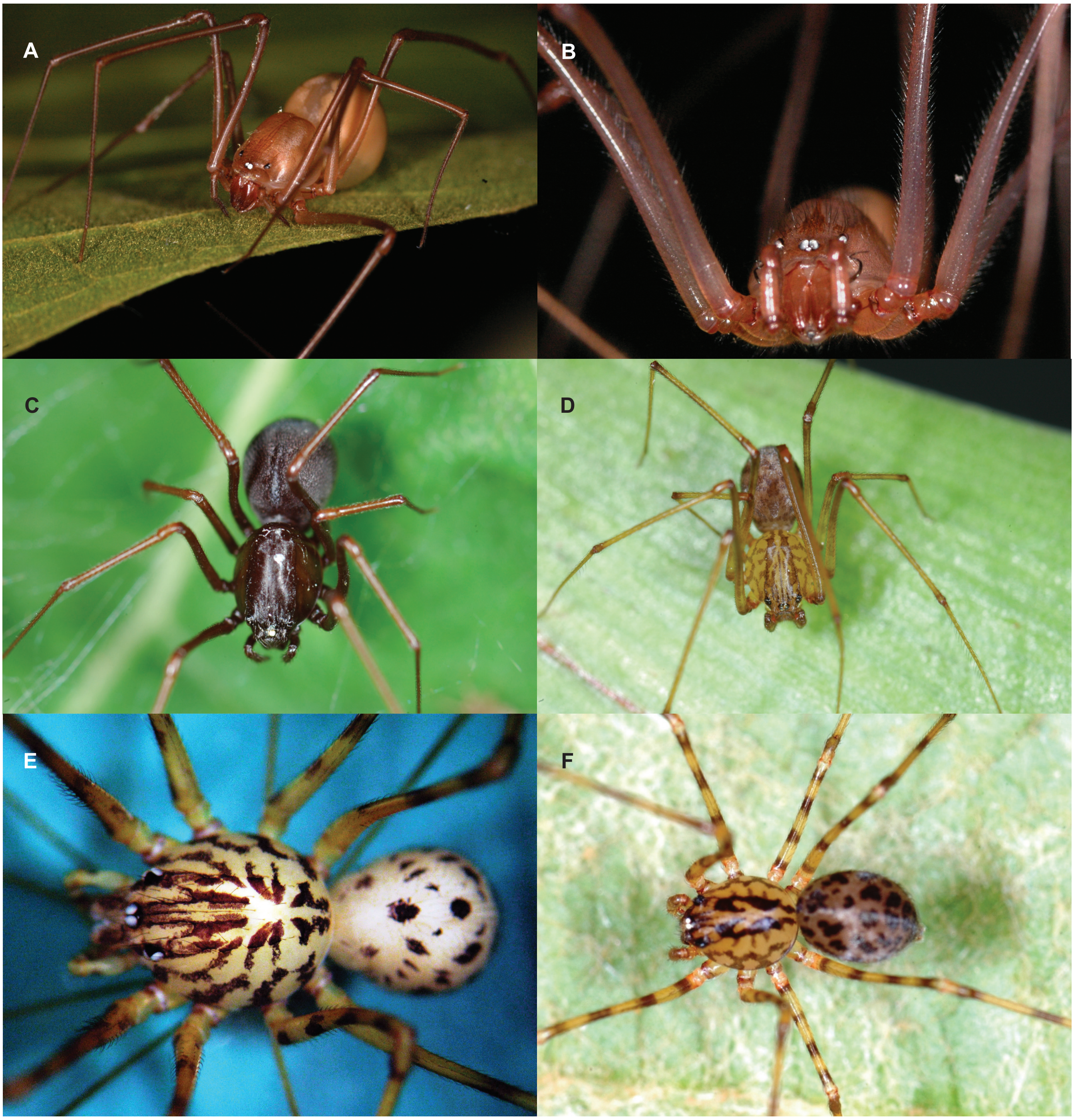

Fig. 1. Four species of cave scytodid spiders. (A) female and (B) male *Scytodes magna*, body length = 10.5 mm; (C) female and (D) male *S. fusca*, body length = 5.8 mm; (E) female Philippines *Scytodes* sp. 2, body length = 5.6mm; and (F) female *S. cavernarum*, body length = 5.3 mm.

from becoming adults. Unless qualified, 'male' and 'female' referred to adults. No individual spider was used in formal observations more than once per day. Decisions such as which particular spider was used in a given observation were made randomly. All experiments were carried out between 1100 h and 1800 h.

For determining the type of social organisation of each species, eleven behavioural traits were considered: (1) the presence/absence of maternal care (e.g. egg-sac guarding); (2) the presence/absence of extended maternal care (i.e. juvenile aggregations maintained beyond the time when they are physiologically and morphologically capable of dispersing from the natal site due to receipt of protection and nourishment from the adult female (Miller, 1989)); (3) the presence/absence of group foraging behaviour; (4) natal dispersal patterns (i.e. do the spiderlings disperse from their natal nest in their early instars or remain until maturity, and does the dispersal follow a progressive sigmoidal function similar to that of *Amaurobius ferox* spiderlings (Kim, 2000)?); (5) adult-juvenile and juvenile-juvenile interactions (i.e. social signals used between conspecifics such as aggressive interactions between siblings); (6) mean total number of spiderlings/female; (7) mean number of spiderlings/clutch produced by a female; (8) the time interval between clutches (egg-sacs); (9) the time interval between the hatch date and next egg-sac production; (10) time elapsing before spiderlings hatched; and (11) mean number of clutches produced by a female. We also recorded the behaviour of the hatchlings immediately upon emergence (i.e. whether they attached themselves to the broken egg-sac or mounted the mother's body, and whether they aggregated around the mother in the natal nest or scattered around the cage). We predicted that the spiderlings of the social scytodids would cluster as a group staying close to the mother for protection, upon eclosion.

We used the expression 'higher level of sociality' when the following would be present: (1) maternal care by guarding their egg-sacs against predators and parasites; (2) extended maternal care in the form of food provisioning (capturing prey and transporting it back to the natal nest for the brood to feed); (3) cooperative prey capture and food-sharing among siblings; (4) delayed juvenile dispersal due to benefits such as receiving more nutrition and hence being able to attain a larger body size before leaving the natal web; (5) the maternal female would share her prey with spiders that did not help in prey capture; (6) spiderlings that capture prey would share it with the other non-captors; (7) little or no cannibalism amongst siblings (cannibalism that does occur is seen only in later instars); (8) females producing fewer offspring (hypothesis: this is a consequence of more time and more effort being invested in the young which should ensure greater survivability amongst them, thus increasing her fitness); and (9) longer intervals between hatching and the next clutch due to the aforementioned hypothesis (the previously stated hypothesis (8) is the rationale for this criterion).

Maternal care of eggs. **–** Cages (220 ×120 × 60 mm) were set up for observing maternal care of eggs for each species. One day after females reached maturity (i.e. undergo their final moult), they were individually housed and maintained in the cages for seven days, during which they built a web in their cage. Soon after the female built her web, a male was introduced into the cage and allowed to mate with the female. The male was then removed from the cage. The mated females were then monitored daily until they produced eggs and also until the eggs hatched. We recorded the date of egg production, the presence/absence of egg-sac guarding, the attendance duration if present, the number of hatchlings, and details of the female's egg-sac guarding behaviour.

Maternal care of offspring: mother-offspring interactions. **–** For determining whether females provided food for their spiderlings, and whether spiderlings shared prey with females instead of females consuming the prey alone (i.e. not allowing the spiderlings to gain access to the prey), the females with their egg-sacs maintained in the laboratory were used. They were monitored daily until the spiderlings emerged from the egg-sacs. The date of emergence, number and instar of hatchlings, and behaviour of hatchlings immediately after eclosion were recorded. After emergence, general brood care of the spiderlings (e.g. food provisioning) by the female were observed for 30 min daily for the next 28 days or until all the spiderlings dispersed to build their own webs. Large prey in the form of house flies (*Musca domestica*) and cricket nymphs (*Gryllus dimaculatus*) were offered to the females and then mother-offspring interactions including female food provisioning and offspring sharing food with their mother were recorded. Food provisioning by the maternal females could take the form of passive prey provisioning (i.e. regurgitation or capturing and wrapping the prey and then leaving it at the site of capture for the offspring to feed). Data on mother-offspring interactions was collected from the same colonies as those that were used for natal dispersal trials (see below).

Natal dispersal pattern. **–** To determine natal dispersal of spiderlings, we designed a 'cage within a cage' experiment (a vertical cage measuring 10 × 10 × 5 cm, with plastic frame and removable glass slides, inside a tupperware which had a hole cut out and covered with a piece of wire gauze (this allows for air movement) (Fig. 2). This experimental design was adapted from Ruttan (1990). To ensure that the dispersal was intrinsic and not due to other causes such as the absence of the maternal female, we used colonies that contained both the female and her spiderlings. The spiders were provided fruit flies ad lib. once a week. Spiderlings were considered "dispersed" when they moved from the inner cage into the outer cage. The outer cage was monitored daily. Spiderlings found in the outer cage were removed, scored as having dispersed on that date, and weighed. For determining whether the cause of death was cannibalism or some other natural causes, dead spiders were checked under the microscope. Spiders that had been cannibalized were easily identified by the presence of silk wrapping and a characteristic shrunken appearance (Yap & Li, 2009). A few individuals always remained within the maternal web for up to several months after their siblings had dispersed. Based on these observations, we defined the end of dispersal as when at least one week had elapsed with only three or fewer individuals remaining in the maternal web. Species that showed both of two criteria were not considered in this experiment: (1) ≥ 50% of the spiderlings dispersed before they were 3-weeks old. We assumed these species to have low tolerance among siblings and hence dispersed early; and (2) ≥50% of the spiderlings within the colony were cannibalized before the end of the third week of emergence.

Group foraging behaviour. – To determine whether spiderlings participated in cooperative prey capture and fed as a group, they were put randomly into cages (10 × 10 × 5 cm) in groups of one, two, three, four, six and eight individuals 20 days after their emergence from egg-sacs (all in the late second instar). There were three replicates for each group. If an individual died during the experiment we replaced it with a new one. Before the start of the experiment the spiderling was weighed to ensure uniformity in size among the spiderlings (e.g. *S. fusca*: mean weight ± 1 SD = 1.14 ± 0.18 mg; ranging from 0.91 to 1.39 mg; 1.3 mm in body length, *n* = 5). The experiment started one day after the introduction of the spiderlings into their cages. The trials began immediately after a house fly was introduced into the cage and lasted 180 min, after which observations were made sporadically in the next 24 hrs. We define 'captors' as individuals that attacked and fed subsequently on the prey, and 'intruders' as those that did not participate in the capture but fed on the paralysed prey. If spiders fed together, we recorded how the prey was captured, paralysis latency (defined as the interval between the introduction of prey and the time when feeding began), the number of attackers (i.e., the number of spiderlings that spat at the prey), and whether or not the captors chased away the intruders. The presence of any aggressive behaviour (defined as forelegs raised and/or waving or a sudden forward jerk towards the counterpart) was also noted. Besides observing behaviour directly, we also video-recorded the sequences seen.

Juvenile-juvenile interactions: sibling tolerance and cannibalism. – For determining whether cannibalism among sibling would occur, sibling groups, each comprised of 10 spiderlings (of approximately the same body size), were assembled in small vertical cages (10 × 10 × 5 cm) 7 days after their emergence (*n* = 3). All groups were provided with 20 fruit flies once a week. This feeding regime was to simulate low-prey conditions so as to investigate whether, under such conditions, siblings would withhold kin cannibalism (i.e. demonstrate high level of tolerance) or readily feed on each other to prevent starvation (i.e. low tolerance level). Each group was observed twice daily for a period of 14 days and thereafter once daily for 28 days. During each observation, the number of spiderlings that died from cannibalism or other causes was noted. Since scytodids prefer live prey (Li et al., 1999), it was presumed that the number of spiderlings that were eaten by their siblings after they died was small.

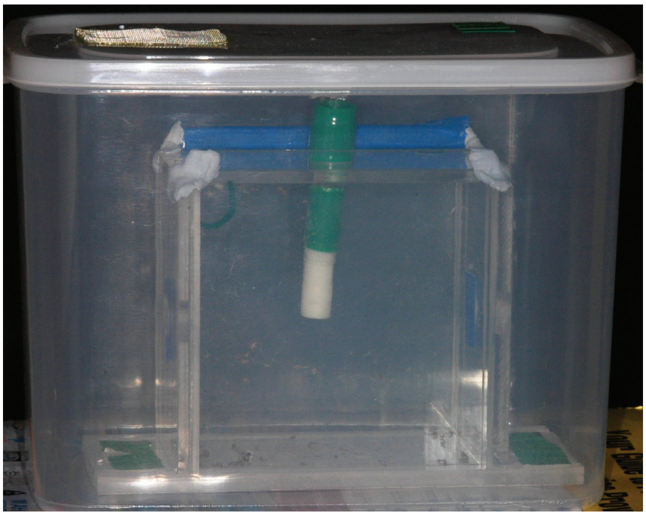

Fig. 2. The 'cage within a cage' set-up for studying the natal dispersal patterns of scytodid spiders. Modified from Ruttan (1990).

Reproductive behaviour. – The mated females (same ones that were used for 'observation of maternal care of eggs') were observed weekly and six variables were examined for each of five cave species: number of clutches (i.e., egg-sacs) per spider, number of spiderlings per clutch (i.e., egg-sac), total number of spiderlings produced by a female throughout her reproductive life-span, time for spiderlings to hatch (i.e. the interval between egg-laying and egg hatching), the interval between clutches, and the interval between hatching and subsequent egg-sac production.

Data analyses

Data were checked for normality by using Kolmogorov-Smirnov tests and analysed with parametric or nonparametric procedures depending on which was appropriate. We performed linear regressions to examine the relationships between the timing of juvenile natal dispersal and juvenile body mass for each species. We also performed multivariate analysis of variance (MANOVA) to examine the differences in six reproductive traits (total number of spiderlings, time taken for spiderlings to hatch, number of clutches, number of spiderlings per clutch, the time interval between clutches, and the time interval between the emergence of spiderlings and the next egg-sac production) among five species. If a significant overall difference was detected, one-way ANOVA was then conducted for each reproductive trait, followed by Tukey's HSD. All tests were two tailed and the data is reported as mean ± S.E. of untransformed data. All statistical analyses were conducted using IBM SPSS Statistics 19 (SPSS Inc., USA).

RESULTS

Colony survey. – The nest structures of the five cave species of scytodids are presented in Table 2. *Scytodes magna* and Guangxi *Scyloxes* sp. 1 that were observed during the survey were either a single adult male or female, or a female carrying an egg-sac. Penultimate males and females made up approximately 18% of the total nest inhabitants of Guangxi *Scyloxes* sp. 1. On a few occasions, *S. fusca* and *S. cavernarum* females were found with newly emerged spiderlings (Table 2).

Table 2. Data on the inhabitants of the five cave scytodid species nests in the field collected over a 7-day period.

Nest inhabitant(s)		*Scytodes fusca* (*N* = 53)	*Scytodes cavernarum* (*N* = 48)	The Philippines *Scytodes* sp. 2 (*N* = 12)	Guangxi *Scyloxes* sp. 1 (*N* = 34)	*Scytodes magna* (*N* = 18)
Mature female	alone	15	22	5	7	5
	alone with egg-sac	9	5	0	0	0
	with spiderlings (1st instar only)*	5	2	0	0	0
	with spiderlings (mix of 1st instar and later)	0	0	0	0	0
	with spiderlings (later instar only)	0	0	0	0	0
	with mature male	0	0	0	0	0
	with mature male with egg-sac	0	0	0	0	0
Mature male	alone	4	4	1	4	2
	with spiderlings (1st instar)	0	0	0	2	0
	with spiderlings (mix of 1st instar and later)	0	0	0	0	0
Groups without adult	1st instar spiderlings without adult	0	0	0	3	0
	1st instar spiderlings and later without adult	0	0	0	0	0
	later instar spiderlings without adult	0	0	2	0	0
Spiderlings	1st instar spiderling alone	0	0	0	0	0
	2nd instar and beyond spiderlings alone	20	15	4	10	11

*spiderlings emerge as 1st instar for these species

Maternal care. – *Scytodes cavernarum*, *S. fusca* and the Philippines *Scytodes* sp. 2 produced eggs throughout the year in the laboratory, whereas *S. magna* and Guangxi *Scyloxes* sp. 1 females produced only 1–2 egg-sacs in the laboratory. *S. cavernarum*, *S. fusca* and the Philippines *Scytodes* sp. 2 females practised maternal care by carrying their egg-sacs in their chelicerae (Fig. 3) whereas females of *S. magna* and Guangxi *Scyloxes* sp. 1 did not carry their egg-sacs in their chelicerae, but instead they hang their egg-sacs in the centre of the web, attached by several threads (Fig. 3). However, *S. magna* and Guangxi *Scyloxes* sp. 1 females always remained in close proximity to the egg-sac, with their bodies touching or almost in contact with the sac (Table 3). There was a difference in the type of egg casing. In *S. magna* and the Guangxi *Scyloxes* sp. 1, their eggs were surrounded by dense amount of thick silk, while in the other three species of *Scytodes*, their eggs were wrapped in a fine, more loosely woven silk envelope (Fig. 4).

When capturing prey, all *S. fusca* ($n = 15$) and the Philippines *Scytodes* sp. 2 females ($n = 8$), and 93% of *S. cavernarum* ($n = 14$) females were observed to drop their egg-sacs first. They usually left the egg-sacs in their maternal nest or suspended them by a thread and then spat at the prey (e.g., house flies) (Fig. 5). Upon subduing the prey the females usually transported it back to where they had left their egg-sacs and then started feeding on the prey. When the cage was tapped or moved, the females usually abandoned feeding and returned immediately to their egg-sacs and carried them again (Table 3). However, *S. magna* and Guangxi *Scyloxes* sp. 1 females rarely dropped their egg-sacs to catch prey. Instead, they usually ignored the prey (Table 3).

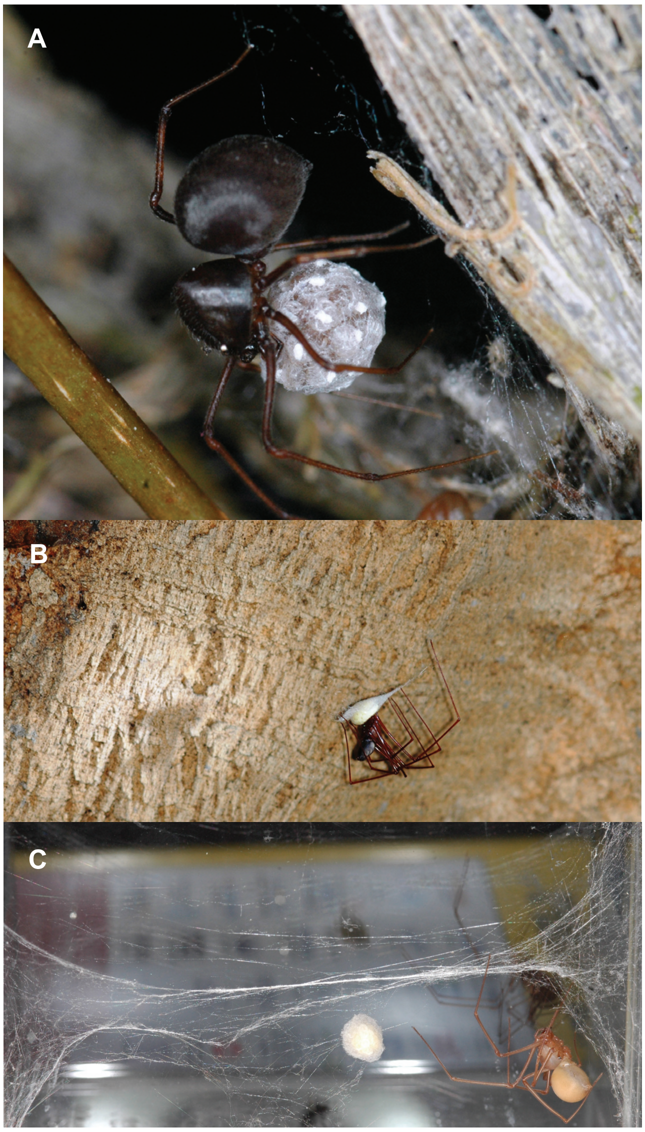

Fig. 3. Maternal care of egg-sacs in spitting spiders. (A) *Scytodes fusca* female carrying her egg-sac in her chelicerae. (B) Guangxi *Scyloxes* sp. 1 female on the surface of the outer cave walls, staying close to her egg-sac. The egg-sac is suspended by two to three threads. (C) Web constructed by *S. magna* female. Her egg-sac is suspended by a few threads at the centre of the web.

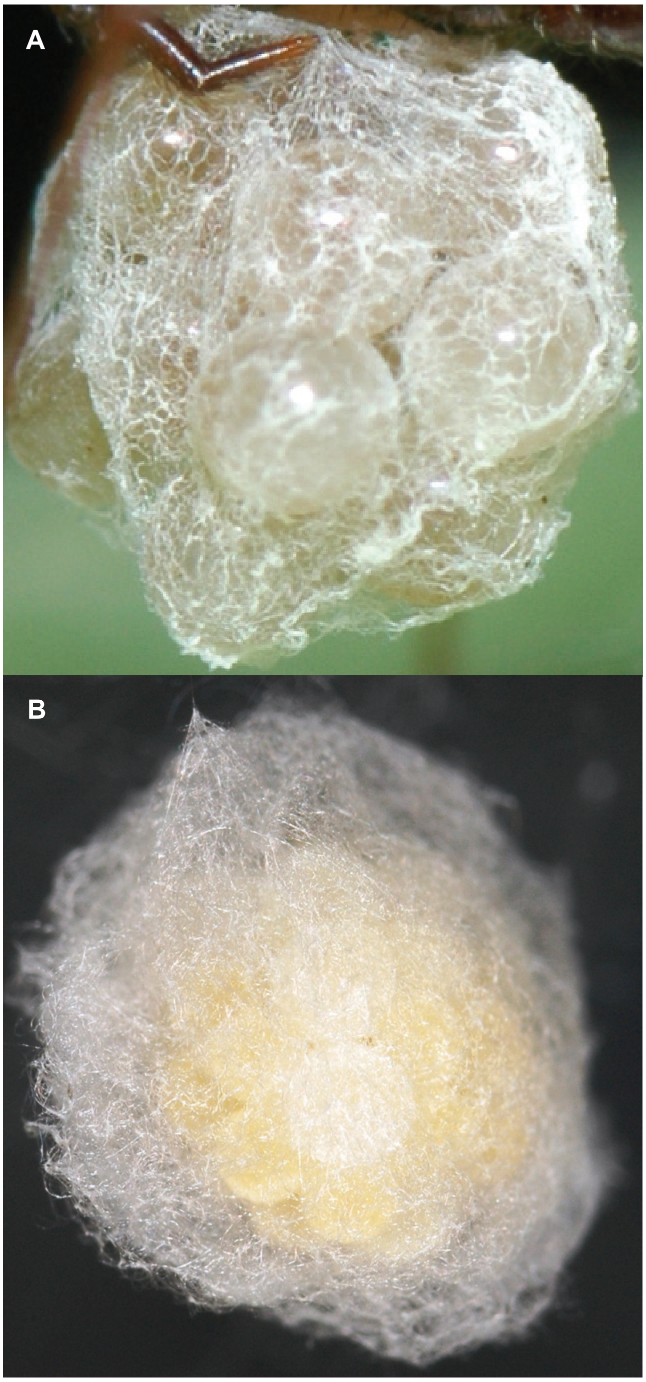

Fig. 4. Scytodid egg-sac. (A) Typical egg-sac of *Scytodes cavernarum*, *S. fusca* and the Philippines *Scytodes* sp. 2; and (B) *Scytodes magna* egg-sac. Note the denser silk surrounding the eggs of *S. magna*.

Table 3. Presence and absence of maternal care of egg-sacs and foraging during egg-sac attendance in the five cave scytodid species.

	Scytodes magna	Guangxi *Scyloxes* sp. 1	*Scytodes cavernarum*	*Scytodes fusca*	Philippines *Scytodes* sp. 2
Carrying egg-sac in the chelicerae	No	No	Yes	Yes	Yes
Foraging during egg-sac attendance	No	No	Yes	Yes	Yes

Emergent phase and emergent behaviour. – The spiderlings of all five cave species emerged as first instars and underwent their first moult into second instars between 3 to 6 days of emergence. Immediately upon emerging from the egg-sacs the spiderlings usually attach themselves to the broken sacs. Within 24 hours, all the spiderlings of *S. magna* and Guangxi *Scyloxes* sp. 1 spread themselves around the cage although still within close proximity to the mother. However, in *S. cavernarum*, *S. fusca* and the Philippines *Scytodes* sp. 2, about half the spiderlings still clustered in the maternal nest and the rest spread out in the cage.

Extended maternal care: food provisioning. – Food provisioning (here we define it as the activity of supplying food items to the spiderlings by capturing of prey, injection of digestive enzymes and eliciting the spiderlings to feed on the captured prey) by females was absent in all five cave species. The females always captured the house fly and fed on it alone (Fig. 6). If the spiderlings approached the feeding female, the female usually raised the first pair of legs to chase them away. However, spiderlings of these five cave species were observed to scavenge on the prey remains. Should the spiderlings capture their own prey regardless of prey type (i.e. fruit flies or house fly), the females never snatched the prey away.

Fig. 5. *Scytodes fusca* female leaving her egg-sac aside to forage on the house fly.

Natal dispersal. – A spiderling's dispersal timing is positively correlated with its body mass in four out of five species except for *S. cavernarum* (Fig. 7). Light (small) juveniles dispersed earlier than heavier juveniles. The first spiderling to disperse was at third instar in *S. magna* (Fig. 7D), Guangxi *Scyloxes* sp. 1 (Fig. 7E) and *S. cavernarum* (Fig. 7B), at mid/late second instar in *S. fusca* (Fig. 7A), while for the Philippines *Scytodes* sp. 2 the first disperser was at early second instar (Fig. 7C). Although the first spiderling to disperse in the Philippines *Scytodes* sp. 2 was around 5 days after emergence from the egg-sac, the majority of the spiderlings dispersed after 47 days of emergence when they have undergone their third moult to become fourth instars. In *S. fusca*, after the first spiderling had dispersed many spiderlings followed suit with a large number of the spiderlings dispersing on day 10 (Fig. 7A).

Group foraging behaviour. – Nothing that clearly qualifies as cooperative prey capture was found in any of the five cave species. If the prey was too large for any one individual to subdue, it was eventually ignored. When the prey was captured by a spiderling, the captor never allowed the prey to be shared. It usually chases the intruders away by displaying sudden jerking movements (i.e. as if the captor is about to lunge onto the intruder) or leg raising and waving. In several instances, however, we observed one or two intruders feeding alongside the captor. This occurred when the prey was too

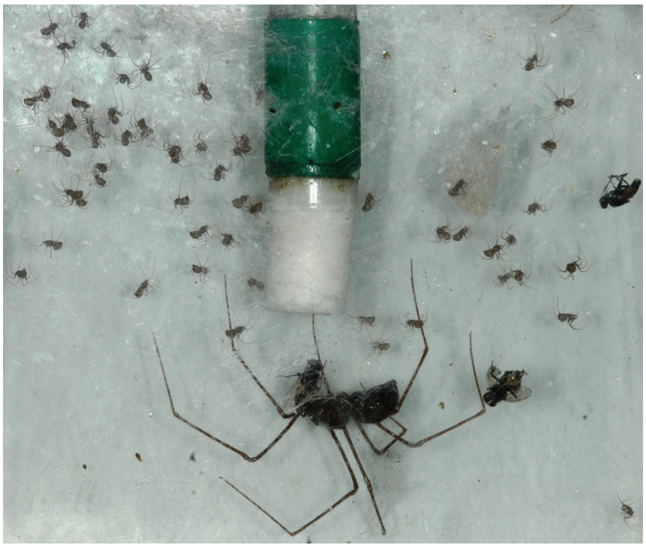

Fig. 6. Newly emerged Guangxi *Scyloxes* sp. 1 spiderlings spread out on the sparse silk nest, and female feeding on house fly alone. Body length of adult female = 11.5 mm.

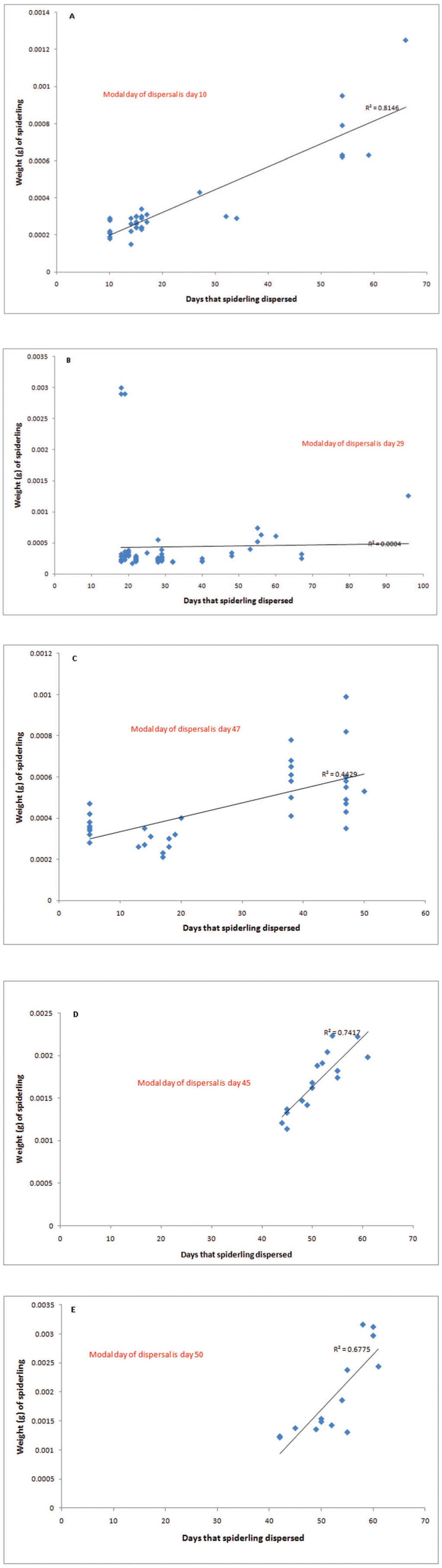

Fig. 7. Relationship between the days in which spiderlings dispersed and spiderling mass in five cave scytodid species. (A) *Scytodes fusca*; (B) *S. carvernarum*; (C) Philippines *Scytodes* sp. 2.; (D) *S. magna;* and (E) Guangxi *Scyloxes* sp. 1.

large (e.g. house fly) to be monopolized by one spider and the intruders always "sneaked" in after the captor had settled down and was busy feeding on the prey.

Cannibalism among siblings. **–** Cannibalism among siblings started 1–2 weeks after emergence from egg-sacs (i.e. about the second instar) in all five cave species (Table 4). Most of the mortality was due to cannibalism. The causes of incidental mortality could be due to death during moulting or starvation due to the incapability of capturing fruit flies when they were small.

Reproductive traits. **–** MAVONA revealed a significant overall difference in reproductive traits among the five species of cave scytodids (Wilks' $\lambda = 0.029$, $F_{24,60.} = 4.415$, $P < 0.001$). There were significant differences in the egg hatching time, the interval between clutches, and the interval between hatching and next egg-sac production. However, no significant differences in the total number of spiderlings produced (Fig. 8A) and the number of spiderlings per clutch (Fig. 8F) were found among the five species (Table 5).

DISCUSSION

Almost every nest of each of the five species surveyed in the field nests was occupied by only a mature male or only a mature female, except that sometimes there was an egg-sac or a group of first-instar spiderlings in the nest with a mature female. Mature females in nests accompanied by later-instar spiderlings were never seen. The hypothesis suggested by these observations is that nests are founded by solitary individuals and offsprings disperse early from the maternal nest. Laboratory observations and experiments also suggest that extended maternal care, maternal food provisioning, cooperative prey-capture and food sharing among siblings are absent in all of the five species of cave scytodids and that there is only a low level of tolerance among siblings. Therefore, 'asocial' appears to be an appropriate term for the cave scytodids. Prey scarcity in the caves may make it difficult for spitting spiders to attain sociality. In the entrance zones, there are numerous aerial prey items but these prey tend to be small (Gillieson, 1996). In the dark zones, there are larger prey but these tend to be scarce (Gillieson, 1996). Small prey items such as fruit flies and mosquitoes can be easily caught by singleton scytodids and would be insufficient for sharing. On the other hand, while prey in the dark zones are of larger size, it also coincides with the fact that the *S. magna* and Guangxi *Scyloxes* sp. 1 scytodids found in this part of the cave are large-sized, again offsetting the potential for sharing to be advantageous. Furthermore, since prey are in low density in the dark zones, there may be considerable competition for these prey items. Rector (2009) studied *Meta ovalis*, a spider that lives in different parts of caves. In the dark zone, *M. ovalis* tend to be sparsely spaced, whereas those in the entrance zones are nearer to each other. As a hypothesis, a similar pattern observed for *S. magna* and Guangxi *Scyloxes* sp. 1 implies that prey scarcity probably leads to spiders opting for a solitary life strategy. The smaller species of scytodids in this study (i.e. *S. fusca*, *S. cavernarum* and Philippines *Scytodes* sp. 2) utilise cracks and crevices in the cave walls possibly as protection from predators and the changing environment. Perhaps insufficient space is another reason why sociality has not evolved in these species of *Scytodes*.

The subsocial pathway is a hypothesis in which it is proposed that the precursor of sociality in spiders is extended parental care, with the juveniles tending to remain in their mother's nest until they develop into later instars (Li et al., 1999) and the subsequent delay in natal dispersal (Buskirk, 1981; Crespi & Choe, 1997). There was no evidence of extended maternal care in the form of prey provisioning in any of the five species of cave scytodids. Maternal care ends at the point where the female aids in the emergence of the spiderlings by tearing open the silken egg case. Maternal females neither provided food nor shared meals with their offspring. If spiderlings were capable of catching their own prey (e.g., fruit flies), the mother never snatched the prey item away. However, siblings may often try to gain a free meal (i.e., intruders try to share the prey item with the captors).

While *S. cavernarum*, *S. fusca* and the Philippines *Scytodes* sp. 2 practised maternal care by carrying their egg-sacs in their chelicerae, *S. magna* and the Guangxi *Scyloxes* sp. 1 stayed in close, persistent contact with their egg-sacs without carrying them. This is the first report of a spitting scytodid not carrying its egg-sac in its chelicerae. Whether it is carrying egg-sac in the chelicerae or maintaining close persistent contact with the egg-sacs, maternal care may be of importance in these five species because potential egg predators such as cave crickets are common in the caves (Machado & Oliveira,

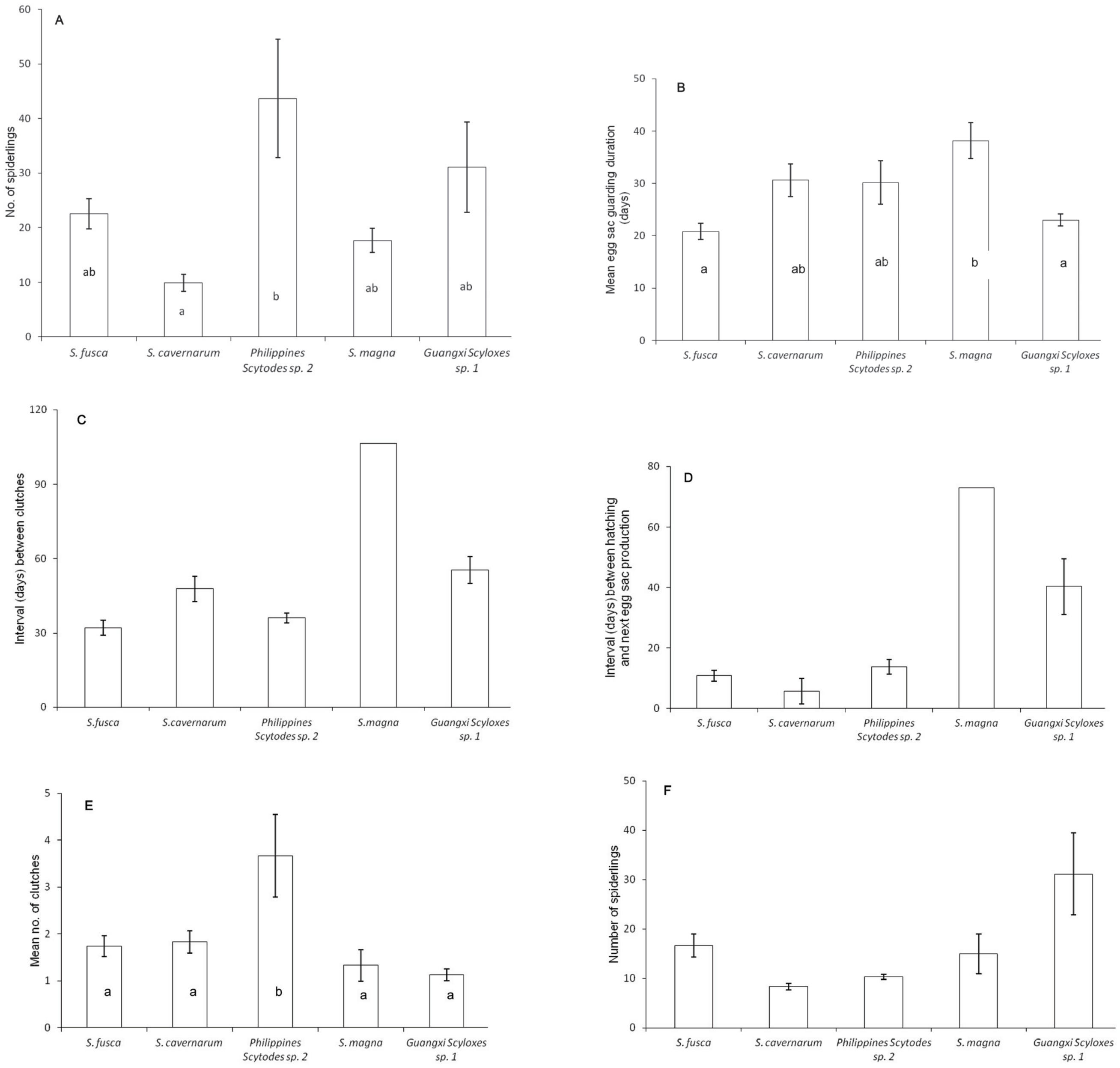

Fig. 8. Reproductive traits of five cave species of scytodids. (A) Mean (± S.E.) total number of spiderlings per female; (B) mean (± S.E.) egg hatching time (d); (C) mean (± S.E.) interval (d) between clutches; (D) mean (± S.E.) interval (d) between hatching and the next egg-sac production; (E) mean (± S.E.) number of clutches; and (F) mean (± S.E.) number of spiderlings per clutch. Different lower cases indicate significant differences.

Table 4. Total cumulative mortality resulting from cannibalism in groups of spiderlings (three groups, 10 spiderlings per group except for *S. cavernarum* in which there were 8 spiderlings per group).

	Week 2 (7–13d)	Week 3 (14–20d)	Week 4 (21–27d)	Week 5 (28–34d)	Week 6 (35–41d)	Week 7 (42–48d)	Incidental mortality*
Guangxi *Scyloxes* sp. 1	0	2	5	9	17	22	4
S. magna	0	3	7	13	19	19	5
S. cavernarum	2	5	9	12	14	18	2
S. fusca	5	10	16	19	19	22	5
Philippines *Scytodes* sp. 2	3	7	10	15	19	21	7

*Incidental mortality refers to deaths not attributed to cannibalism (e.g. from moulting).

Table 5. Results from MAVONA comparing six reproductive traits among five cave scytodids.

	F	*df*	*P*
Total number of spiderlings	2.308	4, 22	0.09
Egg hatching time (d)	4.138	4, 22	0.012
Interval (d) between successive clutches	19.965	4, 22	< 0.001
Interval (d) between hatching and next egg-sac production	20.175	4, 22	< 0.001
Number of clutches (i.e. egg-sacs)	2.851	4, 22	0.048
Number of spiderlings per clutch	2.307	4, 22	0.09

1998). It has been argued that the evolution of parental care is favoured especially when unprotected eggs are highly vulnerable to predators (Wilson, 1971). The fauna inside the caves have bias toward predators (Machado, 2002) and the scarcity of food and the strong predation pressure combined probably leads to a situation in which maternal care confers particularly strong benefits to both mother and offspring. Although extended maternal care is absent in *S. magna* and Guangxi *Scyloxes* sp. 1, the first occurrence of natal dispersal in these two species was at the third instar (i.e., around day 40) (Fig. 7D and E). This seems to imply that, although females do not provide food to their progeny due to reasons discussed above (i.e. prey scarcity and prey not large enough to be shared), they may tolerate their progeny remaining in their webs until they are more physiologically prepared for leaving the nests. In this way, the maternal web may offer protection to young spiderlings.

S. magna and Guangxi *Scyloxes* sp. 1 females rarely leave their egg-sacs to forage, but foraging during egg-sac attendance was frequent in *S. fusca*, *S. cavernarum* and the Philippines *Scytodes* sp. 2. As the latter three species usually build their nests inside the crevices, the deep retreats (L-MYL Yap, personal observations) where a female probably leaves her egg-sac may serve as a natural barrier to egg-sac predators such as cave crickets and ants. *S. magna* and Guangxi *Scyloxes* sp. 1 females with their persistent close contact to their egg-sacs may indeed eat nothing during this period by remaining inactive as spiders that remain inactive have low energy requirements. During times of starvation they can reduce their metabolic rate (Anderson, 1974).

Tolerance, defined as abandonment of mutual aggression, has often been considered to be important in the evolution of spider sociality (Kullman, 1972; Buskirk, 1981; D'Andrea, 1987; Whitehouse & Jackson, 1998). However, cannibalism in the early stages seems to be pronounced in all five species of cave spitting spiders, implying that tolerance among siblings is lacking in these species. Low prey supply has been hypothesized as a condition that can result in spiders readily cannibalizing each other (Avilés & Gesley, 1998).

Low level of tolerance may be an obstacle in the evolution of sociality in cave spitting spiders. Why does pronounced cannibalism occur in cave spitting spiders? There are two possible reasons (Polis, 1988): a direct metabolic gain by eating the conspecific, and an indirect gain by reducing potential competitors thereby diminishing possible negative effects from interference competition (e.g. contest for nest sites). Our results suggest that the direct metabolic gain from eating a conspecific could be of particular importance during the early stages when individuals have not accumulated sufficient fat reserves necessary to withstand periods of food stress in caves. A large number of incidental mortality due to starvation, even in the laboratory where abundant prey was provided, led to this hypothesis.

Resource competition, mate competition and inbreeding avoidance have been proposed as three major ultimate causes of natal dispersal (reviewed in Johnson & Gaines, 1990). The resource competition hypothesis states that siblings disperse in order to avoid competing with each other for resources in resource-limited habitats (Hamilton & May, 1977) and predicts an absence of sex-biased dispersal when they have similar resource requirements (Gandon, 1999). The mate competition hypothesis suggests that individuals disperse to avoid having to compete with siblings for mates, and predicts that the sex suffering the higher cost from intrasexual mate competition will disperse further (Moore & Ali, 1984). The inbreeding avoidance hypothesis suggests that individuals disperse in order to avoid mating with their siblings (Gandon, 1999). The natal dispersal patterns varied among these five species of cave scytodids. The first *S. magna* spiderling to disperse occurred at the third instar yet cannibalism commenced as early as in the second instar phase. A similar trend was observed in Guangxi *Scyloxes* sp. 1. In the Philippines *Scytodes* sp. 2, *S. fusca* and *S. cavernarum*, the first dispersal occurred at the early second instar, late second instar and third instar stage, respectively. If we consider the time in which 50% or more of the spiderlings had dispersed, the Philippines *Scytodes* sp. 2, *S. fusca* and *S. cavernarum* spiderlings dispersed at day 37, 18 and 29, respectively, which equate to the late third instar, late second/early third instar and third instar in the same order. Thus, the general pattern observed is that spiderlings remain in the maternal nest and disperse at a later instar despite the high rates of cannibalism among siblings. Why is this so? It may be possible that spiderlings that have not moulted into third instars are physiologically incapable of spitting and attacking their own prey due to under-developed glue glands or legs that are not strong enough, resulting in uncoordinated movements. Laboratory observations showed that early second instar spiderlings were unable to capture fruit flies. It may be that the early dispersers of the batch may either be fitter or they simply disperse a short distance away from the maternal nest, locate the first available site and remain there until the next moult when they are capable of capturing prey. Following or during dispersal, siblings may still compete for nest sites or resources. Such competition would be reflected in greater dispersal distances when over time the number of dispersing siblings increases and nearby sites become occupied. Spiders may also compete with individuals dispersing from neighbouring nests (Powers & Avilés, 2003). Other spiderlings that remain in the maternal nest have to play a game of cat-and-mouse: avoid being eaten or be the "eater". Spiderlings that successfully cannibalize their siblings obtain more nutrition, thereby attaining a larger body size. These fitter spiderlings may have a higher chance of surviving and reproducing once they disperse from the maternal nest. We therefore suggest that natal dispersal in these five species of cave scytodids primarily reflect competition for resources within the natal nest.

Solitary spiders are expected to produce large numbers of spiderlings compared to social species because an increase in investment per individual young is often associated with a decrease in the number of offspring produced (Schneider, 1996). Due to a lack of extended maternal care, spiderlings tend to have lower survival rates, hence there may be a selection for more clutches and a larger clutch size. Our results show that the Philippines *Scytodes* sp. 2 and Guangxi *Scyloxes* sp. 1 females produced many spiderlings throughout their reproductive phase. However, there was no statistical differences in the mean total number of spiderlings produced by females among the five species (Table 5). Results for the Philippines *Scytodes* sp. 2 is consistent with the hypothesis that clutch size in spiders is correlated with sociality (Kullmann, 1972; Smith, 1982) and parental care (Buskirk, 1981). With a mean of 3.33 clutches/female, this species has the highest clutch number (although not the highest clutch size) and in turn the highest fecundity rate among the five cave scytodids . Being a solitary species, the Philippines *Scytodes* sp. 2 produces more progeny due to the low investment put into each of her offspring. Based solely on the fecundity, however, it is difficult to conclude whether the other four species are solitary or not because the clutch size and clutch numbers are low, which is a character normally used to define the more social spiders.

The results for *S. cavernarum* contradict with our prediction because with each of the females producing a mean of only nine spiderlings in total, this species has one of the lowest fecundity and fertility. One possible reason is that of the five species, *S. cavernarum* females are the smallest in body size (mean body length = 5.3 mm). Fecundity tends to be correlated with body mass in invertebrates, including spiders (Higgins, 1992; Schneider, 1996), therefore a low body size and mass may have resulted in a lower oviposition potential in *S. cavernarum*.

Social spiders are expected to delay egg production if females are performing maternal care, resulting in a longer interval between clutches. However, the interval between the emergence of spiderlings and the next egg-sac production varied among the five solitary species although the intervals were longer in *S. magna* and Guangxi *Scyloxes* sp. 1 compared to the other three *Scytodes* species. One would assume that this could be due to females of *S. magna* and Guangxi *Scyloxes* sp. 1 investing more time in their previous clutch of offspring. However, this was not the case because extended maternal care was absent in all five species. We postulate that the low metabolic rates of these two troglobitic scytodid species may be the cause of the females taking more time to produce another clutch. Carbon dioxide concentration is often significantly higher in caves than on the surface, especially in deep cave passages that have abundant decaying organic material (cited in Howarth, 1983). The relatively higher carbon dioxide and lower oxygen concentrations in the underground environments may play a role in the lowered metabolism (Howarth, 1983). Troglobites often display a much reduced basal metabolic rate compared with their surface relatives, which has been interpreted as an adaptation for greater efficiency in their energy-poor environment (Poulson & White, 1969).

With food scarcity in the caves, it is not surprising that the maternal females do not provide food to their young and cannibalism among siblings is rampant. Perhaps cave spiders are not predisposed to evolve into social species because the presence of groups would be too conspicuous and may inadvertently become an advertisement for potential cave predators. Many social spiders such as *Stegodyphus* and *Anelosimus* spp. are web-builders that have an incentive to form large colonies with extensive webs: to ensnare larger (usually flying) prey. An extensive web structure, which has often been hypothesized to be a prerequisite for sociality in spiders, as it provides a means of communication, is absent in the five cave scytodids. Instead, they construct rudimentary webs in dark and elusive locations such as holes and crevices.

It is interesting to note, however, that sociality can exist in cavernicolous arachnids, for example, in *Goniosoma* harvestmen. Machado (2002) suggested that the subsocial behaviour present in *Goniosoma* may confer a special advantage in this particular environment. *Goniosoma* females care for the eggs and first instar spiderlings before they disperse. Maternal care is crucial for egg survival since predators may consume entire batches in a single night (Machado & Oliveira, 1998). Up to 200 individuals can form diurnal aggregations, and this gregariousness confers defensive advantages to an individual harvestmen. Machado (2002) also proposed that the gregarious behaviour in *Goniosoma* may be induced primarily by microclimatic factors such as relative humidity and temperature, such that gregariousness could act as a behavioural mechanism for regulating and reducing evaporation among grouped individuals.

Prey availability may be the most significant factor in determining mutual tolerance in spiders (e.g. Rypstra, 1986). Two lines of thoughts emerge here: the first one puts a premium on the benefits that the members of the colony may gain through extension of maternal care and avoidance of kin cannibalism. This may lead to cooperative hunting which is hypothesized to be an evolutionary trait of sociality in certain animal groups (Packer & Ruttan, 1988). By contrast the second line of thought puts a premium on the ecological constraints limiting the likelihood that an individual will stay home and form groups. The second line may be applied to these cave scytodids because cooperative hunting via an extensive web structure is not feasible for cave spiders. Moreover, Schneider (1996) has shown that single spiders always gained more mass than spiders in groups, suggesting costs of competition. Witt et al. (1978) also showed that social spiders digest prey more slowly than solitary ones possibly due to spiders in groups injecting less digestive enzymes than when feeding alone. In a prey-scarce, predator-abundant environment such as caves, going solo might be the best survival plan.

In conclusion, all five cave scytodid species have been found to be asocial, although all females have been observed to practise maternal care in the form of close egg-sac attendance. We suggest the possibility that the solitary strategy adopted by Guangxi *Scyloxes* sp. 1, *Scytodes cavernarum*, *S. fusca*, *S. magna* and the Philippines *Scytodes* sp. 2 can be attributed to insufficient food supply and high predation risks.

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