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Maternal Care in Spiders

Bachelor's thesis

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Abstract

Maternal care is any behaviour of the mother which directly benefits its offspring usually at the cost of future reproduction of the female. Many types of maternal care are known among spiders, but a comprehensive review of all different types of maternal care across spider diversity is still largely missing. With the summarisation of research concerning maternal care and thanks to the implementation of genomic data and subsequent advances in spider systematics and evolutionary research, different types of maternal care are interpreted in an evolutionary context and mapped on the up to date phylogenetic tree. Guarding behaviour is common across spider families. On the contrary, various forms of feeding are rare. Some phenomena (matriphagy and regurgitation) evolved repeatedly in distantly related spider families.

Abstrakt

Mateřská péče je chování matky, které přímo prospívá potomkům většinou za cenu budoucí reprodukce samotné matky. Mnoho druhů mateřské péče je známo mezi pavouky, ale shrnující studie všech různých druhů mateřské péče u pavouků zatím nebyla vytvořena. Pomocí shrnutí výzkumů zabývajících se mateřskou péčí a pomocí implementace genetických dat a pokroků v systematice pavouků a v evolučním výzkumu různé druhy mateřské péče jsou interpretovány v evolučním kontextu a zmapovány na aktuálním fylogenetickém stromu. Hlídní je časté chování napříč čeleděmi pavouků. Naopak různé formy krmení jsou vzácné. Některé fenomény (matrifagie a regurgitace) se vyvinuly několikrát u nepříbuzných čeledí pavouků.

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1 Introduction

1.1 Parental Care Overview

Parental care is defined as any behaviour of the parents which directly benefits the offspring usually at the cost of the future reproduction of parents (Trivers 1972). It varies among the whole animal kingdom (Royle et al. 2014). The ancestral state of parental care is no care at all. Parental care for eggs is favoured via selection if the absence of care would lead to a low survival rate (Royle et al. 2016). The origin of parental care was thus likely preceded by ecological factors decreasing offspring survival (Royle et al. 2016). The result of parental care is an increase in fitness in the offspring (Klug and Bonsall 2010). The increase in fitness should however outweigh the costs. The conflict between sexes' fitness or between the fitness of parents and offspring imposes limitations on the evolution of their behaviour. Parenting behaviour is thus influenced by adaptive plasticity (Kölliker 2012; Royle et al. 2014).

The care can be provided by one of the parents (unisexual care) depending on the sex if it is maternal or paternal, by both parents (biparental care), or by parents and nonparents (cooperative care) in social species (Royle et al. 2014). Mothers are the most common carers across the majority of taxa even though males can be as effective as females (Royle et al. 2016).

The evolution of parental care among animals is not yet fully understood. There is still debate about e. g. the origin of mainly biparental care in birds. Biparental care is less common in all other groups of animals except birds (Wesołowski 2004). Modern reptiles usually show minimal effort given into parental care (Blrghardt 1977). However, there are paleontological proofs of parental care in Archosauria, for example, a fossil of *Oviraptor* lying on a clutch of eggs (Clark et al. 1999). Brooding in birds may thus have originated in

theropod dinosaurs (Prum 2002). Fishes show social behaviour and complexity of parental care. In mammals, there is extended biparental or maternal care (Kölliker 2012).

Among invertebrates, there are many groups with unique parental care (Wong et al. Kölliker 2013). Parental care in insects comprises all stages, from no care, which is the most common, through uniparental care to biparental care (Gilbert and Manica 2015). There is a slightly different evolution of parental care between Holometabola and Hemimetabola in insects. In Hemimetabola, biparental care appears to be more stable in the evolution of parental care (Gilbert and Manica 2015). An interesting example of maternal care is the terrestrial staphylinid beetle *Bledius spectabilis* (Wyatt 1986). Females of this species construct bottle-like burrows with narrow entering for themselves and their eggs in the intertidal saltmarsh. The females can close the burrow and reopen it at low tide. Besides guarding and defending against flooding, anoxia, and predators, they also provide the larvae with algae as a main source of food (Wyatt 1986).

Similarly, in some crab species, the females provide oxygen to the embryos via brooding (Fernández et al. 2000).

1.2 Characterisation of Spiders (*Araneae*)

Spiders (*Araneae*) are an order of the class Arachnida which comprises at least 10 other orders: Palpigradi, Scorpiones, Pseudoscorpiones, Solifugae, Ricinulei, Amblypygi, Schizomida, Thylephonida, Opiliones and Acari (Coddington 2005a). However, some authors consider Acari as two independent orders (Dunlop and Alberti 2008; Van Dam et al. 2019), while others argue for including Xiphosura in the arachnids (Lozano-Fernandez et al. 2019).

Spiders represent the second most diverse order after Acari (P. R. Harvey, Nellist, and Telfer 2002; Coddington 2005a). Currently, there are 50 975 species of spiders according

to the World Spider Catalog (<https://wsc.nmbe.ch/> 2023, 18th March) and the number of species continually increases.

Spiders are ecologically diverse predators that usually employ their typical characteristics – web spinning and venom production in prey capture (Foelix 2011). All spiders are gonochorists with sexual dimorphism. Females are usually larger than males and in groups with good vision males often have vivid colours for attracting the opposite sex or as an instrument in competitive interactions with other males (Shamble et al. 2009; Taylor, Clark, and McGraw 2011).

Although there are studies concerning maternal care in spiders, they are usually focused on one target species or genera. A comprehensive review of all different types of maternal care across spider diversity is still largely missing. Thanks to the implementation of genomic data and subsequent advances in spider systematics and evolutionary research, different types of maternal care can be interpreted in an evolutionary context. The main objectives of this bachelor thesis are to: a) summarize the published data concerning maternal care in spiders and b) detect potential behaviour and evolutionary trends in the maternal care by mapping the information obtained from the literature onto an up to date phylogenetic tree.

2 Paternal Care in Arachnids

Paternal care is unusual in arachnids. *Sensu stricto*, paternal care has been observed only in order Opiliones (Machado et al. 2004). However, in some orders, there are hints of male behaviour, which could be beneficial for offspring or future mothers, that I will also discuss in this chapter.

For females, it is rather costly to decide not to care for their brood because the production of eggs is costly energy-wise. On the contrary, the production of sperm is cheap and the only resource that is limited to the males are the females themselves (Wade 2002; Kokko and Jennions 2003). Therefore, deserting the eggs may increase the fitness of a male because he can mate again with another female (Trivers 1972). Because their investment is higher, the females are in the position of the choosing sex and not *vice versa*.

The main differences between maternal and paternal care are the evolutionary traits (Trivers 1972; Wade 2002). Maternal care seems to be driven by natural selection whilst paternal care, exclusive in arachnids to order Opiliones, may be sexually selected behaviour (Machado et al. 2004). This may be because the internal fertilization, common in arachnids (Burger et al. 2006), comes with the uncertainty of paternity (Kokko and Jennions 2003). Reasons for males not being involved may be, besides the reason stated above, that males sometimes die after mating. In some spider species, females consume their mates (Elgar and Fahey 1996; Slater et al. 2005). Additionally, males have naturally a shorter life span, they usually stop feeding during the search for a mate, or may not even feed at all after reaching maturity (Yip and Rayor 2014).

Paternal care in the order Opiliones has evolved at least three times independently in distantly related superfamilies of the suborder Laniatores (Nazareth and Machado 2009). In these groups, females prefer males caring for eggs to noncaring ones (Nazareth and

Machado 2009; Requena and Machado 2015). Males of *Chavesincola inexpectabilis* (Opiliones, Gonyleptidae) occupy and defend nests (Nazareth and Machado 2009). Even though in Opiliones some species have paternal care and some exhibit amphisexual care for example, *Acutisoma proximum* (Gonyleptidae) (Buzatto and Machado 2009), maternal care still prevails (Nazareth and Machado 2009). Amphisexual means that the opposite sex has the potential for developing characteristic behaviour of each sex. Amphisexual care is when a male takes on female parental responsibilities after her abandonment of the offspring.

In Pseudoscorpions (Pseudoscorpiones), parental care is present in all species, but it is mainly exhibited by mothers (Del-Claro et al. 2009). It has been observed that males cooperate by offering their prey to members of the colony including the young without paternity discrimination in *Paratemnoides nidifactor* (Tizo-Pedroso and Del-Claro 2005; Del-Claro and Tizo-Pedroso 2009; Del-Claro et al. 2009). Besides capturing the prey, the males of this species together with non-reproductive females and mothers do the external cleaning of the colony (Tizo-Pedroso and Del-Claro 2011) and exhibit collective defence of the young (Tizo-Pedroso and Del-Claro 2011; 2018).

Females provide all known different types of parental care in spiders. No paternal care in spiders has been observed, but it is known that there is amphisexual care in the orb-weaver *Manogea porracea* (Araneidae) and similar cooperative behaviour of both parents has been observed in the permanently social velvet spider *Stegodyphus dumicola* (Eresidae) (Moura et al. 2017; Kürpick 2000; Yip and Rayor 2014).

In the case of *Manogea porracea*, as amphisexual care is taken the construction of a web by a male above the female web with eggs (Moura et al. 2017) because males can in the absence of the mother take on her responsibilities. Males of this species are valuable for protecting offspring against predators and parasitoids with the same efficiency as

females alone. There is no significant difference between maternal care and the care of both parents in the case of *M. porracea*. Therefore, male investment in parental care occurs efficient only in the absence of a female. One of the reasons for males to participate in parental care may be an assurance of future copulation (Kürpick 2000; Hunt and Simmons 2002; Moura, Vasconcellos-Neto, and Gonzaga 2017).

Another interesting case of paternal involvement is documented from the sand dwelling wolf spiders *Allocosa brasiliensis* (Lycosidae) (Aisenberg et al. 2011) and *Allocosa alticeps* (Lycosidae) (Aisenberg and González 2011), which evolved a reversed sex role, including courtship behaviour and reversed sexual dimorphism (Aisenberg et al. 2007). Males are larger than females which is rare in spiders (Moya-Laraño et al. 2002). Females of these species search for male burrows and initiate courtship when they find one. After copulation, males leave the female inside the burrow and enclose the entrance with the cooperation of the female. Female spiders stay in the closed burrow alone (Aisenberg et al. 2007). In these species, the males are in the position of a choosing sex (Aisenberg and González 2011).

3 Maternal Care in Spiders

After oviposition, eggs are protected by cocoons made from the mother's silk. These cocoons (also called egg sacs), can be carried around, left unattended, or be guarded by the spider mother (Suter et al. 1987; Ruhland et al. 2016) and defended in times of need (Fink 1987; Castanho and Oliveira 1997; Viera and Romero 2008).

Maternal care sometimes does not end with the care for the egg sack. It can also be extended to the offspring after hatching (Yip and Rayor 2014). The females can provide offspring with further defence (Schneider 1995), brooding care (Ruhland et al. 2016), and food supply (Evans 1998). In this thesis, the maternal care is considered both care for the eggs before hatching and the care for the offspring (Eason 1964; Guo et al. 2021).

3.1 Cocoons Production and Care

Cocoons are silken sacs made by female spiders to protect their eggs (Opell 1984). The construction is a complicated process which differs among species. After choosing the oviposition site the spider constructs a silken basal plate with cylindric walls (Japyassú et al. 2003; Foelix 2011). Then it lays eggs on the basal plate. The liquid coating around the eggs starts to harden. It dries up. Subsequently, the female constructs a so-called "cover plate" as a barrier between the eggs and the environment. The cover plate is a silken horizontal wall that encloses the eggs and provides further protection (Opell 1984; Foelix 2011; Japyassú et al. 2003).

Females use their silk glands for producing different types of silk. Based on differences in thread diameter, function, production, and visual aspects, spider silk falls into three categories: fine, coarse, and tufted silk (Opell 1984).

Some taxa make only single-layered egg sacs from fine silk. Others add a layer of coarse silk, tufted silk, or both above the first layer. Both coarse and tufted silks can be

used for camouflage. Fine silk comes from the tubuliform glands. Coarse and tufted silks are products of ampullate glands (Opell 1984).

The egg sacs may have many different shapes, sizes, and colours that are species-specific. It is also not rare for cocoons to change colour over time (Ewunkem and Agee 2022).

The most important function of a cocoon is likely delaying water loss (Hieber 1992). Besides preventing desiccation, the egg sacs silk also helps to protect eggs from microbial infections and predators (Opell 1984; Viera and Romero 2008; Ponte et al. 2021; Ewunkem and Agee 2022). Such protection however does not work in cases of spider-specialized predators, *e. g.* Mantispidae (Viera and Romero 2008; Ewunkem and Agee 2022).

3.1.1 Oviposition Site Selection

The selection of the oviposition site is crucial because most spiders do not move their eggs after depositing them so this choice may affect the survival of offspring (Morse 1993). The oviposition site must meet the physical conditions needed for the development of the eggs (Morse 1985). Web-building spiders do not only choose an oviposition site, they choose a foraging site for their offspring too. The web made for the egg sac is also used by the offspring (Suter et al. 1987).

A similar situation happens with the crab spider *Misumena vatia* (Thomisidae) which lays and hides eggs between the leaves of milkweed (Morse 1985). Mothers of this species chose a nest site near the future hunting sites for spiderlings (Morse 1993). For choosing the nest sites, females have to move from their last hunting side. After emerging, it is easier for spiderlings to obtain enough feeding opportunities which has a positive effect on their fitness. Sites with good hunting conditions for adult spiders differ from good hunting

sites for juveniles because of their physical differences. The placement of the nest site also affects the probability of parasitism and predation pressure (Morse 1985).

For spiders that are guarding the egg sac after deposition, it is critical to choose the right habitat, which is suitable for the parents and the offspring, because the habitat will influence the fitness of both (Morse 1985; Pike et al. 2012). This can be very tricky. For example, in the flat-rock spider *Hemicloea major* (Gnaphosidae), which lives under rocks, it is very hard to find a habitat with liveable thermal conditions for the female and her offspring (Pike et al. 2012). Females of this species do not move their egg sacs after deposition, and they live in a thermally challenging environment with temperatures above 50°C. Their rock, used as a shelter, must be large and thin for preventing overheating and simultaneously hot enough to fasten the embryonic development of the eggs (Goldsbrough et al. 2004). Besides thermal cues, spiders have other species-specific ecological preferences in retreat site selection (Bilde et al. 2002). Abiotic and biotic conditions of habitat can affect adaptive advantage.

Eggs can be laid inside spiders' retreats, also called egg nests, as seen in jumping spider *Heliophanus cupreus* (Salticidae), or be hung in free hanging structures (Foelix 2011; Hieber 1992). Daddy long-legs spiders (Pholcidae) hold this hanging structure in their chelicerae (Jakob 1991). Pholcids do not only hold the cocoons they also spin special fine silk web domes, which can be later used by offspring before they molt (Sedey and Jakob 1998).

For orbweavers, it is typical to hang cocoons onto the low vegetation or under the bark. *Argiope cophinaria* hangs cocoon on the tops of field grasses. It is supposed to hang securely with balance even in the wind (McCook 1890).

The females of the ogre-faced spider *Deinopis cf. cylindracea* construct spherical brown cocoons which are left hidden by the female in the litter (Ponte et al. 2021a). They

are quite safe left alone, without a guarding mother, because their colour resembles the branches and autumn leaves they are hiding under, and provides them with camouflage.

Some spiders always carry their cocoons wherever they go. Females of the spitting spider *Scytodes* sp. carry their egg sac in their chelicerae (Li et al. 1999), the same way as the nursery web spiders Pisauridae do (Fink 1987). Wolf spiders (Lycosidae) carry their cocoons attached to their spinnerets (Eason 1964; Ruhland et al. 2016), and huntsman spider *Heteropoda venatoria* (Sparassidae) carries the cocoon in its pedipalps underneath the body (fig. 1) (Parr 2016).



Figure 1: Female of *Heteropoda venatoria* (Sparassidae) guarding its egg sac by carrying it underneath its body in pedipalps. Taken from Ewunkem and Agee 2022.

Female spiders usually care only for their own cocoons, but mothers of *Loxosceles gaucho* (Sicariidae) can care after foreign egg sacs with the same amount of energy. If they are faced with a choice, they will prefer their own, unless their cocoon is not viable. It

means that some spider species are able to recognize their own cocoons, but do not hesitate to spend energy even on foreign ones (Japyassú et al. 2003).

On the other hand, some spider species are not able to differentiate between cocoons and some spiders, which have multiple egg sacs, tend to desert them (Japyassú et al. 2003; Foelix 2011; Ewunkem and Agee 2022). Generally, the spiders with an one year cycle do not guard their cocoons, and therefore usually produce more than one egg sac (Humphreys 1987). The abandonment of the cocoons after construction is also widely occurring in e.g. orb-weaver spiders (Araneidae) (Mark Harvey et al. 1993), and with some exceptions (Benavides et al. 2017) in the pirate spiders (Mimetidae) (Guo et al. 2021).

Besides ultimate desertion, females sometimes leave their egg sacs only for a while. For example, the females of *Holocnemus pluchei* (Pholcidae) abandon their cocoons only for a brief moment to copulate with males (Calbacho-Rosa et al. 2017). A common behaviour is abandoning the egg sac in defence. For example in the ant-mimicking spider *Aphantochilus rogersi* (Thomisidae), mothers leave their cocoons unguarded and drive ants away by attacking (Castanho and Oliveira 1997a).

Wolf spider mothers are able to recognise if their cocoon is full of living juveniles, or if it is empty, which seem to have the same absence of emitting signals as cocoons full of dead juveniles. In the case of unviable or empty egg sacs, the mothers abandon them (Ruhland et al. 2019). Similarly, abandonment is often in the case of offspring with no chance of survival due to various reasons (Klug 2006). Damaged cocoons by fungi etc. can be recognised by spider mothers, but there are also many other forms, for example, parasites such as Mantispididae, which spider mothers cannot distinguish, and therefore care for the cocoon even if there is no chance of survival for its content (Viera and Romero 2008).

3.2 Defending and Guarding

Spider mothers usually guard their eggs before hatching. Some species continue the guarding after the juveniles hatch, until their first or later molts (Brach 1976), or in some cases into adulthood (Yip and Rayor 2014). Most spiders are solitary and the spider mothers care for the offspring only until they disperse (Eason 1964). Parental care is considered to be one of the first steps on a way toward the sociality of primary non-social species (Viera et al. 2007). Only a minority of species has evolved some sort of social organisation in maturity, but it is more common among siblings and their parent to form a subsociality and stay together before reaching maturity. This subsocial behaviour has been discovered in 18 spider species with no phylogenetic relation. The difference between subsocial behaviour and care for newly emerged spiderlings is the length of the stay together. This care is called transient subsocial behaviour and most authors do not consider it as real social interaction until it is extended beyond the first instar (Yip and Rayor 2014).

In this bachelor thesis, I follow the categorization of transient subsocial behaviour according to Yip and Rayor (2014). They divided transient subsocial behaviour into 3 categories: egg sac guarding, opening the egg sac, and guarding the offspring until the first instar.

3.2.1 Egg Sac Guarding

Aside from egg sac carrying species, the guarding of the egg sac is usually happening in one place. Females guarding their egg sacs may simply position themselves near their clutch, or they can construct a protective shelter for both themselves and their egg sacs. For example, females of the bromeliad-living jumping spider *Psecas chapoda* (Salticidae) construct their cocoons in the middle of a leaf of *Bromelia balansae* and subsequently build yet another silk cover above their egg sac and themselves as protection (Viera and Romero 2008). Similar behaviour is known from the families Clubionidae, Anyphaenidae,

and Cheiracanthiidae, which guard their eggs in the nests constructed by silk and rolled-up grass leaves (Humphreys 1987; Toyama 1999). Vegetation is used also by spiders from the genus *Stegodyphus* (Eresidae) as a typical habitat for the construction of their silken nests, but most velvet spiders live under the bark of trees or stones (Sharma et al. 2021). Families Dysderidae and Gnaphosidae also hide under the stones in silken cells (Pike et al. 2012; Sharma et al. 2021).

The presence of a guarding female seems to have two main benefits for eggs; The survival rate of guarded cocoons is higher, and spiderlings emerge later than those of unguarded egg sacs (Fink 1986). Higher mortality in egg sacs, which are not guarded by a spider mother, is caused by predation or sac disappearance (Fink 1986; 1987; Viera and Romero 2008; Yip and Rayor 2014).

For example, unguarded cocoons of the green lynx spider, *Peucetia viridans* (Oxyopidae), break their attachment lines of silk due to abiotic factors and disappear after a while. Disappearance and following death by falling to the ground is prevented by the presence of a guarding mother which can avert dislodgement into a more hostile environment by resuming the tightening of the silk threads (Fink 1987). It was shown that most of the unguarded egg sacs of this species are not able to emerge on their own (Willey and Adler 1989). The same inability of emergence was shown in uncarried cocoons of a huntsman spider *Heteropoda venatoria* (Sparassidae) (Parr 2016).

The obvious reason why the presence of adult spider is decreasing the mortality of eggs is defending them against predators, such as ants or araneophagic spiders (Fink 1987; Willey and Adler 1989; Viera and Romero 2008). The already mentioned green lynx spider can defend its eggs against ants by direct attack or by changing the position of the cocoon attached to low vegetation by adjusting the silk threads holding it in place. The ants are not only dangerous for the eggs, but also for adult female spiders; however, the mothers do not

hesitate to defend their eggs (Fink 1987; Eason 1964; Viera and Romero 2008; Willey and Adler 1989).

The guarding period is not easy for females because they are willing to risk their own lives in defence of their egg sacs (Viera and Romero 2008). Moreover, the guarding females and non-guarding females of the same species have significant differences in weight changes. Guarding females of green lynx spider feed ten times less than non-guarding ones. The hunger and also the energy expenditure caused by guarding or due to the heaviness of carried eggs lead to a significant loss of weight in females (Fink 1986; Parr 2016). Besides the energy cost of maternal care, it also increases the risk of predation (Royle et al. 2012; Yip and Rayor 2014).

3.2.2 Opening the Egg Sac

In some species, for example in wolf spiders, the spiderlings cannot escape from a cocoon without their mother's help. They are not able to open the egg sac by simply cutting through the egg sac wall with their chelicerae as the spider mother is (Foelix 2011; Eason 1964). Females use their pedipalps and legs for rotation of the egg sac, and tear the silk by chelicerae along the white seam of the cocoon (Ruhland et al. 2016).

In the case of nonviable egg sacs, mothers of the wolf spider *Pardosa saltans* (Lycosidae) tend to abandon their cocoons right before the time of emerging, and do not try to tear it beforehand (Ruhland et al. 2019). The females are informed by tactochemical stimuli of the cocoon about the state of their eggs' development (whether the juveniles are alive, or not) in the postembryonic period (Ruhland et al. 2019). After the emergence of juveniles, females of *P. saltans* end egg sac care and stop carrying the empty cocoons, which would otherwise lead to wasting their energy. On the other hand, in the cob web spider *Anelosimus* cf. *studiosus* (Theridiidae), the opening of the egg sac and juvenile emergence seem to be more dependent on mechanical movement of the juveniles inside the

cocoon and neuroendocrinal mechanisms of the mother, than chemical stimulants (Viera et al. 2007).

When the spiderlings' emergence is dependent on the mother's help, the loss of the mother usually has a significant impact on the viability of the young. In the green lynx spider, the loss of a mother does not need to lead to the death of juveniles but in most cases, it does. In below 30% of cases, the spiderlings were able to make exit holes in the cocoon wall, but even in these cases they usually got trapped in them and could not escape (Willey and Adler 1989). Similar records are known from observations of the species *Cheiracanthium japonicum* (Cheiracanthiidae), in which offspring were not able to successfully emerge without the attendance of their mother (Toyama 1999).

In some other species, even though it was shown that the spiderlings can tear the cocoon silk, their mothers open the cocoon themselves. Such behaviour has been reported in the huntsman spider *Heteropoda venatoria* (Sparassidae) (Ross et al. 1982; Parr 2016).

3.2.3 Guarding the Offspring until and after the First Instar

After emerging from the cocoons, the spiderlings usually stay together until the first instar. The first instar is the developmental stage of the spiderlings that follows after the first molt, usually occurring inside the egg sac (Yip and Rayor 2014). Until the first instar, the guarding is considered to be transient subsocial behaviour. Afterwards, it is considered subsocial behaviour (Yip and Rayor 2014).

The care for the offspring may involve many different behaviours displayed by the female. One of the reasons for guarding the offspring is the same as for guarding the egg – to decrease predation and mortality (Fink 1986; Willey and Adler 1989). Mothers are able to chase and kill some of the predators (Schneider 1995; Yip and Rayor 2014). Therefore, they increase offspring survivability.

The second reason for guarding the offspring is the securing of nests or other habitats (Sedey and Jakob 1998). It has been shown that guarded spiderlings take a longer time before dispersing than those unguarded ones (Fink 1986). This difference in dispersal may be caused by differences in adult and juvenile silk. Juvenile silk is finer, it is thus more advantageous for juveniles to use sturdier webs provided by their mother (Kaston 1987; Fink 1986). For example, in the subsocial spider *Amaurobius ferox* (Amaurobiidae), it has been shown that parental webs inherited from mothers are more efficient in prey capture than webs constructed by juveniles (Kim et al. 2005). Moreover, the spiderlings can save energy by using the already existing webs (Jakob 1991).

In nursery web spiders, the females construct a tentlike web for their egg sac when they are finished with the period of carrying it around in their chelicerae. It is the last act of maternal care towards their soon emerging spiderlings who can use this web until their first molt (Foelix 2011). For that reason, the pisaurids are also referred to as the “nursery web spiders” (Yip and Rayor 2014). Natal webs constructed by pholcids for their offspring to use before dispersing have a similar function (Jakob 1991; Sedey and Jakob 1998).

Carrying offspring as done by spider mothers in wolf spiders is also considered guarding. After emerging, the offspring climb onto the mother’s abdomen, where they continue to be cared for (Eason 1964; Ruhland et al. 2016). They hold onto their mothers’ abdominal setae (Rovner et al. 1973). Carrying the young prevents the mother from predatory behaviour. The reason for that may be the potential loss of spiderling on her back (Ruhland, Pétilon, and Trabalon 2016), or unwanted feeding above her fallen offspring (Eason 1964). Mother rather reduce their basal metabolism and therefore lower their activity (Ruhland et al. 2016). They are capable of fuelling the energy of their own tissues during the brooding period (Ruhland et al. 2016). With the use of silk lines, the spiderlings can travel between the mother and the ground if it is necessary, for example, if they are

dismounted from their mother's abdomen (Higashi and Rovner 1975). In the case of dismounting, the female does not help them to remount (Higashi and Rovner 1975).

In social species, the guarding period is usually prolonged into later instar or even to maturity. Caring for the mature individual is rare in invertebrates, especially in spiders (Royle et al. 2012; Dong et al. 2019). Along with prolonged care comes prolonged feeding and guarding of the offspring (Kullmann 1972). Cooperation plays a key role in social spiders. They built webs together, they provide communal feeding, and most importantly they exhibit collective brood care. Examples of families with collective brood care are the velvet spiders (Eresidae) and funnel-web spiders (Agelenidae), and cob-web spiders (Theridiidae) (Kullmann 1972). In collective brood care adult individual does not care only after their offspring but also after the offspring of others (Kullmann 1972; Lubin 1982).

A main disadvantage of subsocial parental care is possibly the increased risks of predation because larger nests attract more predators, and the energy cost of parental care also leads to weaker mothers (Royle et al. 2012; Yip and Rayor 2014). Guarding females lose significantly more weight than unguarding females. That is mainly because of energy expenditure during guarding and defending, and also because of feeding the offspring (Yip and Rayor 2014; Ruhland et al. 2016). Also, it has been shown that unguarding females have better chances to construct second egg sacs than guarding females (Fink 1986).

The last advantage of the guarding period for offspring is the provisioning of the food supply by the mother (Kullmann 1972). Food provisioning during the gregarious phase exists in various forms in spider families (Yip and Rayor 2014). Of course, there are exceptions, for example, wolf spider females carry their offspring on their abdomen but do not feed them (Ruhland et al. 2016).

3.3 Providing Food Supply

Food is essential for the offspring and for the mother which has a larger energy expenditure due to parental care. Despite the energy cost, the mothers do not usually feed during brood care (Ewunkem and Agee 2022; Ross et al. 1982; Parr 2016). The reason for this may be avoiding the dangerous situations associated with prey attacking (Ruhland et al. 2016).

Offspring of some species must stay inside the egg sac for some time to complete their development. This period is called the larval stage and ends with the first molt into a nymph, which is defined as an individual with functioning venom and silk glands (Ibarra 1985; Foelix 2011). The offspring are fed only by trophic eggs during the larval stage, or not at all (Ibarra 1985; Perry and Roitberg 2006).

In some spider species, the mother provides hatched offspring with food supply. Forms of feeding vary in species from providing trophic eggs, sharing prey, feeding the offspring liquefied food from the midgut, secreting nutritive fluids (milking) to the suicide of the mother which then becomes the offspring's meal (Guo et al. 2021; Dong et al. 2019; Chen et al. 2018).

All types of food provisioning methods have proven to decrease or completely prevent cannibalism between siblings (Bilde and Lubin 2001).

3.3.1 Direct Food Supply

As a direct food supply is considered sharing the prey with the offspring or laying a batch of trophic eggs. These eggs, also called nurse eggs, cannot develop into viable spiderlings and are used by the offspring to feed upon (Perry and Roitberg 2006). They are full of yolk, and therefore very nutritious for spiderlings (Gundermann et al. 1991; Perry and Roitberg 2006). Spider mother deposits trophic eggs either during oviposition into the

cocoon, just before the hatching of the fertilized eggs, or continuously in the course of spiderling development (Gundermann et al. 1991; Perry and Roitberg 2006).

Laying trophic eggs within the egg sac is known from several families, for example in spitting spiders Scytoididae (Hite 1966), cob-web spiders Theridiidae (Valerio 1974), and ground spiders Gnaphosidae (Ibarra 1985; Yip and Rayor 2014), but the consumption of the trophic eggs outside the cocoon has been observed only in funnel-web spiders Agelenidae (Ibarra 1985), crab spiders Thomisidae and lace-web spiders Amaurobiidae (Ibarra 1985; Kim and Roland 2000).

In *Amaurobius ferox* (Amaurobiidae), the offspring stimulate their mother, which could be viewed as begging behaviour, before she begins with laying the clutch of the nurse eggs (Kim and Roland 2000). Mothers after the separation from their offspring do not lay any trophic eggs and rather lay viable batches (Perry and Roitberg 2006; Kim and Roland 2000; Gundermann et al. 1991).

Another direct food provisioning is sharing the prey. In some spiders, mothers feed upon the prey before they share it with the offspring, and in others, female spider only injects saliva which makes it easier for spiderlings to suck out the insides (Kullmann 1972).

The funnel-web spider *Coelotes terrestris* (Agelenidae) guards its cocoon inside a tube-like retreat, and after hatching, it provides spiderlings with an increasing amount of captured prey for about a month (Krafft et al. 1988). Spiderlings of this species stroke their mother in a begging like behaviour until she gives them her prey. By the end of the gregarious phase, spiderlings are able to steal their mother's food by force. The prey handling time by the mother is decreasing; therefore, she has less time to feed on the prey and needs to increase the prey capture to satisfy her needs. Leaving off the captured prey is

also present in other spider species, for example in *Archaeranea wau* Theridiidae (Lubin 1982; Krafft et al. 1988; Foelix 2011).

3.3.2 Regurgitation

Regurgitation is a way of feeding the offspring with liquified food from the mother's midgut. It consists of predigested prey and the mother's own intestinal tissue (Salomon, Schneider, and Lubin 2005). This feeding method does not require spiderlings to use any venom or enzymatic fluids; therefore, they can save energy and resources (Salomon et al. 2005). No species lay trophic eggs and regurgitate at the same time which suggests that these two methods of food provision have the same function, and therefore are mutually exclusive (Yip and Rayor 2014).

Regurgitation is found in two unrelated families cribellate Eresidae (for example in genus *Eresus*, *Stegodyphus*) and ecribellate Theridiidae (for example in genera *Theridion* and *Anelosimus*) (Kullmann 1972; Brach 1977; Foelix 2011). This method of feeding was recognised as an obligatory phase of maternal care in few spider species (Kullmann 1972). It is for example known as an obligatory phase in *Theridion impressum* (Theridiidae) (Kullmann 1972). Regurgitation is typical for social spiders with some exceptions (Lubin 1982), but it can be found in solitary species. Besides families Eresidae and Theridiidae, there is a record of one species in wolf spiders, *Aglaoctenus lagotis* (Lycosidae), which feeds its offspring by regurgitation (Stefani et al. 2011).

The length of regurgitation differs among the species. Some spiders feed their offspring until the first instar, others, for example, *Stegodyphus lineus* (Theridiidae), prolong their brooding care and regurgitate even after the first molt (Kullmann 1972).

Regurgitation has proven to be a good method for fair feeding because mothers give food to spiderlings in portions, and can thus regulate their growth, and reduce size

differences among the offspring (Kullmann 1972; Salomon et al. 2005). The spiderlings are able to beg for food by pushing towards the mother's mouth (Salomon et al. 2005).

Regurgitation does not need to be only towards juveniles. In the genus *Anelosimus* (Theridiidae), there has been observed regurgitation by subadult siblings towards starving individuals (Gómez et al. 2015). It has been shown that males are favoured in feeding from siblings' midgut (Viera et al. 2006). Preference towards male feeding may be aimed towards reaching maturity faster. Males need fewer molts to reach maturity, which is probably a strategy developed to avoid inbreeding in subsocial spiders (Bukowski and Avilés 2002).

3.3.3 Matriphagy

Matriphagy is the consumption of the living mother by its offspring (fig. 2) (Toyama 2001).



Figure 2: *Stegodyphus lineatus* (Eresidae) spiderlings eating their mother by matriphagy. Taken from Royle et al. 2014.

Females provide themselves as a food source willingly (Toyama 2003). They are eaten completely except for the exoskeleton by their offspring which climb onto the female's body and suck out its fluids (Toyama 2003; Salomon et al. 2005; Tripathi et al. 2020).

It is a great sacrifice for the mother because it seems to be present even in mothers, that are healthy and capable of producing the next batch of eggs.

In *Chiracanthium japonicum* (Cheiracanthiidae), matrophagy has been observed even though no other food provisioning method during maternal care is known (Toyama 1999; 2001). The second instar offspring perform consumption of their mother (Toyama 1999). Matrophagy is beneficial for this species, but spiderlings can survive without feeding upon their mother, if the mother is removed, but the offspring without matrophagy tend to disperse earlier, at the second instar, which influences their future survival (Toyama 2001; 2003).

Dispersal from the nests without a mother occurs faster than from those where the offspring feed upon the present mother. However, the orphaned spiderlings are not able to molt into the third molt before dispersal and to grow as fast as the ones with matrophagy occurring inside their nests (Toyama 2001). Delayed dispersal and occurrence of the third molt inside the breeding nests may be also beneficial because spiderlings are always at higher risk during molting. Molting within the nest is therefore safer for them (Toyama 1999).

The two main advantages of matrophagy are the increase of spiderling size before dispersal and the prevention of cannibalism among the siblings (Toyama 2001; 2003). Also, later dispersal in later instars increases the spiderling survival rate, reproductive success, and fitness (Toyama 2001; Kim et al. 2000) because larger females of *C. japonicum* produce more eggs, and larger males have better reproductive chances in the

future (Toyama 1999; 2003). It has been also shown that matrophagous spiderlings are better at prey capture (Kim et al. 2000).

Regurgitation often precedes matrophagy (Salomon et al. 2005), and can be displayed by many species within the same family. In the case of Eresidae, the females of *Stegodyphus lineatus* provide up to 95% of their body mass to their offspring by regurgitation, and the rest is provided by matrophagy (Salomon et al. 2005). This is probably because regurgitated fluid has more nutritional value (Salomon, Schneider, and Lubin 2005). Similar behaviour is also known from *S. pacifus* (Eresidae) (Tripathi et al. 2020). In *S. mimosarum* (Eresidae), regurgitation seems not restricted to mothers but extends to females that show allomaternal behaviour, the care of othermother's offspring (Seibt and Wickler 1987; Junghanns et al. 2017).

Another example of a species with extended maternal care and matrophagy is *Amaurobius ferox* (Amaurobiidae) (Kim et al. 2000), which does not feed the offspring neither by regurgitation nor by sharing its prey. It rather uses trophic eggs (Kim and Roland 2000).

3.3.4 Milking

Milking has been observed in the jumping spider *Toxeus magnus* (Salticidae) (Chen et al. 2018). This type of feeding is provided in the form of nutritive high-protein fluid droplets excreted by the female's epigastric furrow (fig. 3) and sucked out by spiderling (Chen et al. 2018; Dong et al. 2019). The spiderlings of *T. magnus* are not able to survive without milk provisioning. In this species, the milking is extended to the sexually mature offspring (Chen et al. 2018; Dong et al. 2019).

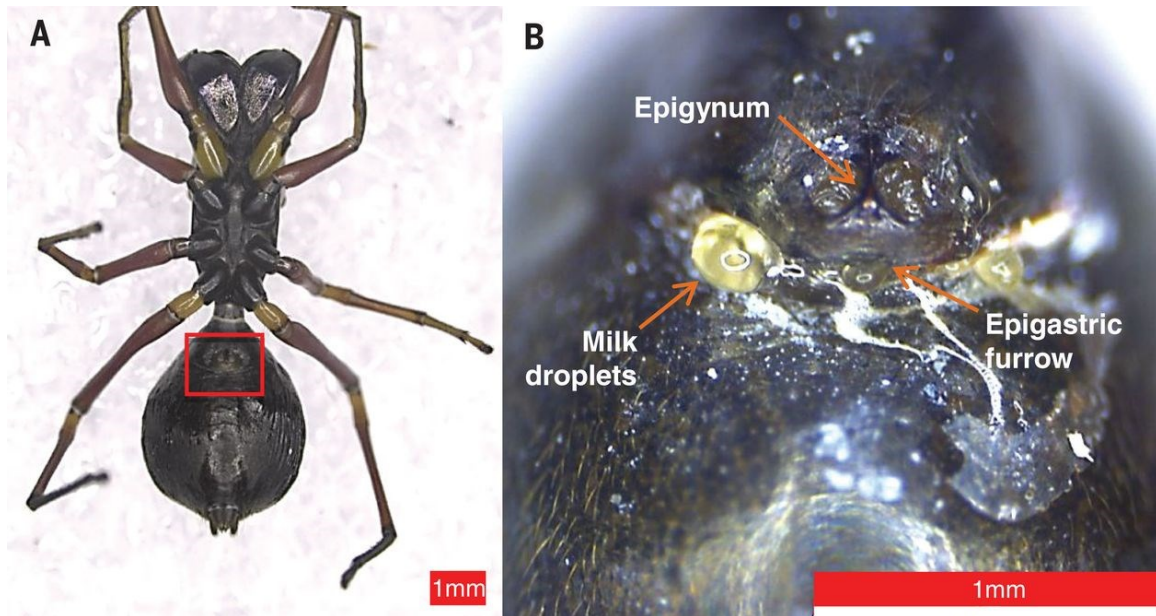


Figure 3: Female of *Toxeus magnus* (Salticidae) producing milk droplets from epigastric furrow. (A) Ventral view of mother. (B) Milk droplets. Taken from Dong. et al. 2019.

The evolutionary mechanisms leading to milking in spiders are poorly understood, but it has been hypothesized that this nutritive fluid could have evolved from trophic eggs (Chen et al. 2018). Lactation in mammals is considered the costliest method of maternal care. The milking in spiders in comparison to the lactation in mammals, does not show any immunological effects (Demmelmair et al. 2017; Dong et al. 2019).

4 Evolution of Maternal Care in Spiders

In this bachelor thesis, maternal care in spiders was divided into 3 main categories: 1) cocoon production and care, 2) defending and guarding, and 3) providing food supply. The production of egg sac is known from all spider families so it is not highlighted in the phylogenetic tree as the other subcategories are. In the second category (defending and guarding), it is distinguished between a) guarding the eggs, and b) guarding the hatched spiderlings, and in the last category (providing food supply), there are various subcategories: a) sharing the prey captures, b) trophic eggs, c) regurgitation, d) matrophagy, and e) milking.

Based on my research, the types of maternal care are summarized in the table (tab. 1), and mapped onto the phylogenetic tree representing our current understanding of spider evolution (fig.4). The phylogenetic topology was created as a consensus of scientific articles (Opatova et al. 2020; Kallal et al. 2021; Azevedo et al. 2022; De Oca et al. 2022) and follows Kallal et al. 2021 in term of the position of the velvet spiders Eresidae and the superfamily Nicodamoidae (but see Kallal et al. 2021 and Kulkarni et al. 2021). Some families are not included in the topology due to the incomplete taxon sampling in the source literature.

In the phylogenetic tree, only the information that could have been obtained via scientific references is shown (tab. 1). Families without any highlighted type of maternal care either do not display any parental behaviour. Families with no data about their maternal care are marked with N/A (not available)

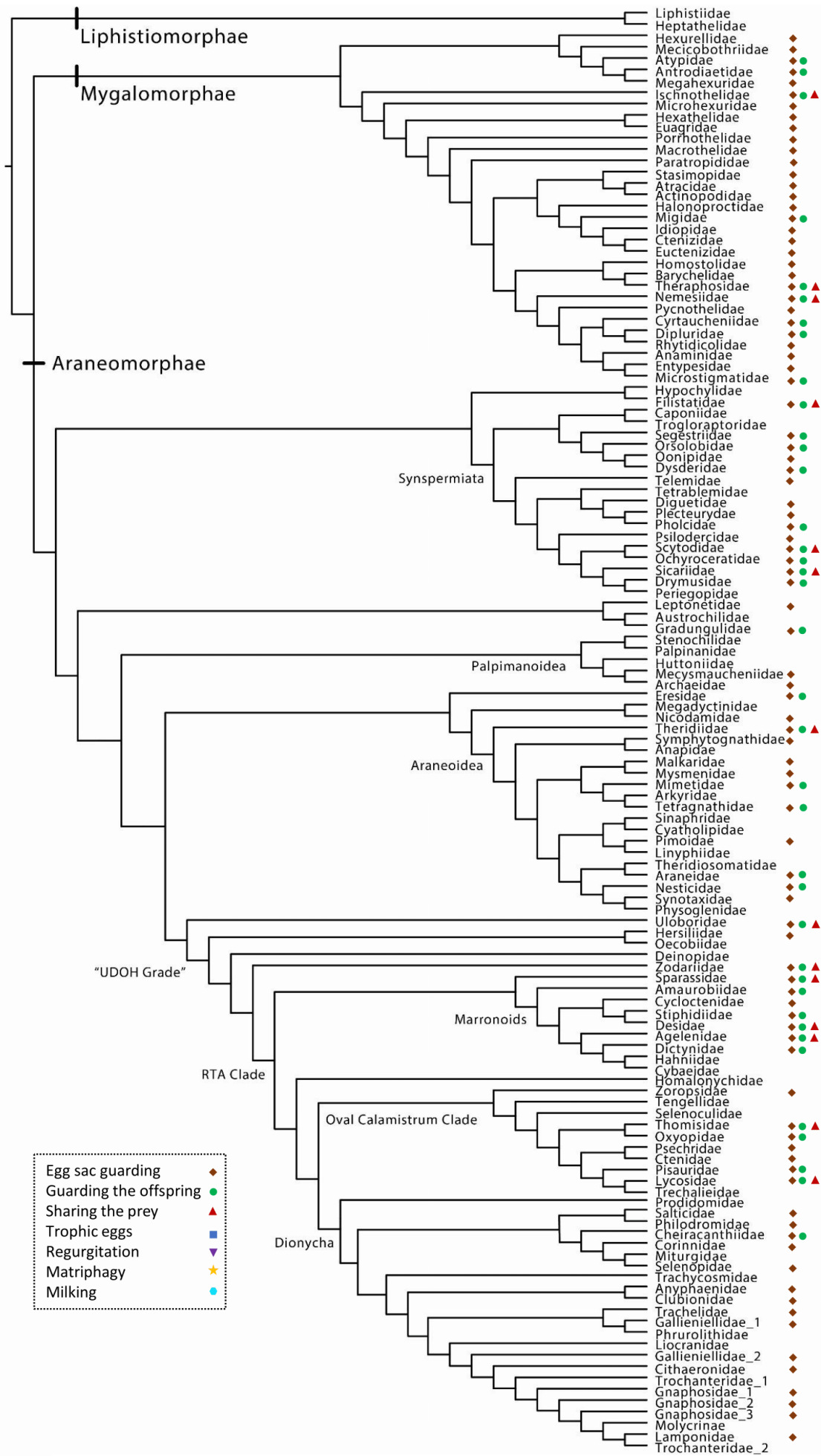


Figure 4: Phylogenetic tree mapping the various types of maternal care in spiders.

5 Discussion

Research concerning maternal care in spiders is a prominent field of behavioural study in arachnology (Yip and Rayor 2014). I hope that in the future we will know more, but at the current state, there is no information concerning maternal care in some spider families.

The most common method of maternal care in spiders besides the construction of the cocoon, which is present in all families, is certainly egg sac guarding. There are no significant differences in the occurrence of guarding across Mygalomorphae and Araneomorphae. Guarding of the eggs is common in both groups.

The food provisioning methods are relatively rare among spider families. As the main food provisioning method, direct food supply is predominant. The most unique type of maternal care is milking in Salticidae (Chen et al. 2018; Dong, Quan, and Chen 2019), but it may have not been discovered in other families yet. Other feeding methods probably evolved more times based on the research.

Regurgitation had to evolve at least in four families independently - once in Oval Calamistrum Clade (family Lycosidae), and at least once in both Eresidae and Theridiidae (Araneoidea clade). In two instances, Eresidae and Theridiidae, regurgitation is also linked with matriphagy (Yip and Rayor 2014). It seems that the presence of regurgitation and matriphagy is related to the social behaviour in Eresidae and Theridiidae (Kullmann 1972; Kürpick 2000). The phenomenon of regurgitation preceding matriphagy was not found in other families, but it may be a consequence of missing data.

Matriphagy had to evolve at least four times in distantly related spider clades (Araneoidea, Dyonicha, Marronoids, and Oval Calamistrum Clade) in the evolution of spiders. In the case of Marronoids, it actually evolved twice within the same clade. There is a possibility of simultaneous evolution of matriphagy within one family in other spider

families, but more research is needed to confirm (Gundermann et al. 1991; Kim et al. 2000).

Matriphagy often pairs with the presence of trophic eggs, precisely in Marronoids (families Agelenidae and Amaubiroidae) (Ibarra 1985; Gundermann et al. 1991; Kim et al. 2000), in Oval Calamistrum Clade (family Thomisidae) (Evans 1998), and in Araneoidae (family Theridiidae) (Valerio 1974; Salomon et al. 2005; Tripathi et al. 2020). Theridiidae is the family with the highest number (seven) of types of maternal care (construction of the cocoons, guarding the egg, guarding the hatched offspring, sharing prey with the offspring, trophic egg, regurgitation, and matriphagy) (Kullmann 1972; Brach 1977; Valerio 1974; Samuk and Avilés 2013; Yip and Rayor 2014).

Cheiracanthidae is the only family showing matriphagy without regurgitation or trophic eggs (Toyama 2001). This may be caused by a lack of information, or it can mean that matriphagy can occur on its own as a method of food provisioning for offspring without preceding trophic egg or regurgitation.

The results confirm that regurgitation and providing food supply by laying trophic eggs do not coexist in one species, but it was observed within one spider family (Theridiidae). This could confirm that trophic eggs and regurgitation can coexist in related species within the same family.

The data obtained by this bachelor thesis is nonetheless valuable and show a new angle upon the evolution of maternal care in spiders.

6 Conclusion

Spiders evolved various methods of parental care to increase the survivability of their offspring. Generally, the guarding of the egg sac or hatched spiderlings seems to be the most efficient in adding fitness contravene to the cost of parents because it is the most common state throughout the spider families worldwide. Extended maternal care including food provisioning methods was observed only in twenty-one families. It seems that the behavioural trend of matrophagy, which evolved at least four times, and regurgitation, which evolved at least four times, evolved independently in distantly related families.

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8 Appendixes

Table 1: Table of obtained information via scientific references about types of maternal care discussed in this bachelor thesis as observed in spiders.

| Family | Cocoon | Guarding the eggs | Guarding the hatched | Sharing prey | Trophic eggs | Regurgitation | Matriphagy | Milking | References |
|------------------|--------|-------------------|----------------------|--------------|--------------|---------------|------------|---------|---|
| Liphistiidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | Guo et al. 2021 |
| Heptathelidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Hexurellidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Mecicobothriidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Costa and Pérez-Miles 1998; Viera and Gonzaga 2017 |
| Atypidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Dippenaar-Schoeman 2002 |
| Antrodiaetidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Coyle and Icenogle 1994 |
| Megahexuridae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Ischnothelidae | yes | yes | yes | yes | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Yip and Rayor 2014; Jantschke and Nentwig 2001; Ghirotto and Guadanu 2021 |
| Microhexuridae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Hexathelidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Euagridae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Porrhothelidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Macrothelidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Wu et al. 2022 |
| Paratropididae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Valdez-Mondragón et al. 2014; |

| Family | Cocoon | Guarding the eggs | Guarding the hatched | Sharing prey | Trophic eggs | Regurgitation | Matriphagy | Milking | References |
|-----------------|--------|-------------------|----------------------|--------------|--------------|---------------|------------|---------|---|
| Stasimopidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Engelbrecht et al. 2012 |
| Atracidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Actinopodidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Ferretti et al. 2013 |
| Halonoproctidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Migidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Dippenaar-Schoeman 2002; Ferretti et al. 2014 |
| Idiopidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Mirza and Sanap 2012 |
| Ctenizidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Euctenizidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Homostolidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Barychelidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Dippenaar-Schoeman 2002; Schwendinger 2003 |
| Theraphosidae | yes | yes | yes | yes | no | no | no | N/A | Yip and Rayor 2014; Viera and Gonzaga 2017; Hüsser 2018; Dippenaar-Schoeman 2002; |
| Nemesiidae | yes | yes | yes | yes | no | no | no | N/A | Buchli 1969; Viera and Gonzaga 2017; Dippenaar-Schoeman 2002 |
| Pycnothelidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Cyrtaucheniidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Dippenaar-Schoeman 2002; Leroy and Leroy 2005 |

| Family | Cocoon | Guarding the eggs | Guarding the hatched | Sharing prey | Trophic eggs | Regurgitation | Matriphagy | Milking | References |
|------------------|--------|-------------------|----------------------|--------------|--------------|---------------|------------|---------|--|
| Dipluridae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Nicoláz 1993; Dippenaar-Schoeman 2002; Ghirotto and Guadanu 2021 |
| Rhytidicolidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Anaminidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Entypesidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017 |
| Microstigmatidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Viera and Gonzaga 2017; Dippenaar-Schoeman 2002 |
| Hypochoylidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Filistatidae | yes | yes | yes | yes | no | no | no | N/A | Cokendolpher and MacDonald 2008, Yip and Rayor 2014 |
| Caponiidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Trogloraptoridae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Segestriidae | yes | yes | yes | no | no | no | no | N/A | Japyassú et al. 2003; Rovner 1986; Tiwari 2021 |
| Orsolobidae | yes | yes | yes | no | no | no | no | N/A | Forster and Platnick 1985 |
| Oonopidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Korenko et al. 2009 |
| Dysderidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Sharma et al. 2021; Rovner 1986 |
| Telemidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Juberthie 1985 |
| Tetramblemidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Diguetaeidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Boulton and Polis 1999 |
| Plecteuryidae | yes | yes | no | no | no | no | no | N/A | Garcia et al. 2020 |
| Pholcidae | yes | yes | yes | no | no | no | no | N/A | Yip and Rayor 2014, Sedey and Jakob 1998; Jakob 1991 |
| Psilodercidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Pérez-González et al. 2015 |

| Family | Cocoon | Guarding the eggs | Guarding the hatched | Sharing prey | Trophic eggs | Regurgitation | Matriphagy | Milking | References |
|-------------------|--------|-------------------|----------------------|--------------|--------------|---------------|------------|---------|--|
| Scytodidae | yes | yes | yes | yes | yes | no | no | N/A | Hite 1966; Yip and Rayor 2014; Perry and Roitberg 2006 |
| Ochyroceratidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Benavides et al. 2017; Silva 2016 |
| Sicaariidae | yes | yes | yes | yes | no | no | no | N/A | Japyassú et al. 2003 |
| Drymusidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Benavides et al. 2017; Silva 2016 |
| Periegopidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Leptonetidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Ledford et al. 2012 |
| Austrochilidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Gradungulidae | yes | yes | yes | no | no | no | no | N/A | Forster and Gray 1979; Doran et al. 2001 |
| Stenochilidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | Guo et al. 2021 |
| Palpinanidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | Guo et al. 2021 |
| Huttoniidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | Guo et al. 2021 |
| Mecysmaucheniidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Wood 2020 |
| Archaeidae | yes | yes | no | no | no | no | no | N/A | Wood 2008 |
| Eresidae | yes | yes | yes | no | no | yes | yes | N/A | Kullmann 1972; Brach 1977; Yip and Rayor 2014; |
| Megadyctinidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Nicodamidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Harvey 1995 |
| Theridiidae | yes | yes | yes | yes | yes | yes | yes | N/A | Kullmann 1972; Brach 1977; Valerio 1974; Samuk and Áviles 2013; Yip and Rayor 2014 |
| Symphytognathidae | yes | yes | no | no | no | no | no | N/A | Coddington 2005; Griswold and Yan 1951 |
| Anapidae | yes | no | no | no | no | no | no | N/A | Kropf 1997 |

| Family | Cocoon | Guarding the eggs | Guarding the hatched | Sharing prey | Trophic eggs | Regurgitation | Matriphagy | Milking | References |
|-------------------|--------|-------------------|----------------------|--------------|--------------|---------------|------------|---------|--|
| Malkaridae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Kallal et al. 2021 |
| Mysmenidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Lopardo and Hormiga 2015 |
| Mimetidae | yes | yes | yes | no | no | no | no | N/A | Guo et al. 2021, Benavides et al. 2017; Silva 2016 |
| Arkyridae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Tetragnathidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Edwards and Edwards 2000 |
| Sinaphridae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Cyatholipidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Pimoidae | yes | yes | N/A | N/A | yes | N/A | N/A | N/A | Mammola et al. 2016 |
| Linyphiidae | yes | no | no | no | no | no | no | N/A | Watson 1998, Kostro-Ambroziak 2020 |
| Theridiosomatidae | yes | no | no | no | no | no | no | N/A | Coddington 2005 |
| Araneidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Yip and Rayor 2014; Harvey et al. 1993; Barnes et al.; Quero et al 2022; Moura et al. 2023 |
| Nesticidae | yes | yes | yes | no | no | no | no | N/A | Carver et al. 2016; Cokendolpher 2007 |
| Synotaxidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Agnarson 2003 |
| Physoglenidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Uloboridae | yes | yes | yes | yes | no | yes | no | N/A | Yip and Rayor 2014 |
| Hersiliidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Baehr and Baehr 1987 |
| Oecobiidae | yes | no | no | no | no | no | no | N/A | Glatz 1967 |
| Deinopidae | yes | no | N/A | N/A | N/A | N/A | N/A | N/A | Barrantes et al. 2014; Ponte 2021 |
| Zodariidae | yes | yes | yes | yes | no | yes | no | N/A | Pekár and Král 2001; Castanho and Oliveira 1997; Traxler 2016 |

| Family | Cocoon | Guarding the eggs | Guarding the hatched | Sharing prey | Trophic eggs | Regurgitation | Matriphagy | Milking | References |
|----------------|--------|-------------------|----------------------|--------------|--------------|---------------|------------|---------|---|
| Sparassidae | yes | yes | yes | yes | no | no | no | N/A | Rowell and Avilés 1995; Parr 2016 |
| Amaurobiidae | yes | yes | yes | no | yes | no | yes | N/A | Kim and Roland 2000; Ibarra 1985; Kim et al. 2005; |
| Cycloctenidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Hickman 1981 |
| Stiphidiidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Vink 2011; Hodge 2007 |
| Desidae | yes | yes | yes | yes | no | no | no | N/A | Downos 1994 |
| Agelenidae | yes | yes | yes | yes | yes | no | yes | N/A | Krafft et al. 1988; Ibarra 1985; Gundermann et al. 1991 |
| Dictynidae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Silva 2016 |
| Hahniidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Cybaeidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Homalonychidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Zoropsidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Dippenaar-Schoeman and Myburgh 2009; Yancey 2018 |
| Tengellidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Selenoculidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Thomisidae | yes | yes | yes | yes | yes | no | yes | N/A | Evans 1998 |
| Oxyopidae | yes | yes | yes | no | no | no | no | N/A | Yip and Rayor 2014; Fink 1986; Willey and Adler 1989 |
| Psechridae | yes | yes | no | no | no | no | no | N/A | Humphreys 1987; Tiwari et al. 2021 |
| Ctenidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Yip and Rayor 2014; Hazzi 2014 |

| Family | Cocoon | Guarding the eggs | Guarding the hatched | Sharing prey | Trophic eggs | Regurgitation | Matriphagy | Milking | References |
|-------------------|--------|-------------------|----------------------|--------------|--------------|---------------|------------|---------|--|
| Pisauridae | yes | yes | yes | N/A | N/A | N/A | N/A | N/A | Yip and Rayor 2014 |
| Lycosidae | yes | yes | yes | yes | no | yes | no | N/A | Stefani et al. 2011; Yip and Rayor 2014; Ruhland 2019; Eason 1964; Ruhland, Pétilon, and Trabalon 2016 |
| Trechaleidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Prodidomidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Salticidae | yes | yes | no | no | no | no | no | yes | Chen et al. 2018; Dong et al. 2019; Yip and Rayor 2014; Viera and Romero 2008; Silva 2016 |
| Philodromidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Hendawy and El-Mezayyen 2003 |
| Cheiracanthiidae | yes | yes | yes | no | no | no | yes | N/A | Toyama 1999; 2001; 2003 |
| Corinnidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Bosselaers et al. 2000 |
| Miturgidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Selenopidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Crews 2023; Villanueva-Bonila 2016 |
| Trachycosmidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Anyphaenidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Zanatta et al. 2016 |
| Clubionidae | yes | yes | no | no | yes | no | no | N/A | Humphreys 1987; Perry and Roitberg 2006; Pollard 1983; Harvey et al. 1993 |
| Trachelidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Bauer et al. 2019 |
| Gallieniellidae_1 | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Goloboff 2000 |
| Phrurolithidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Liocranidae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Gallieniellidae_2 | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Goloboff 2000 |

| Family | Cocoon | Guarding the eggs | Guarding the hatched | Sharing prey | Trophic eggs | Regurgitation | Matriphagy | Milking | References |
|------------------|--------|-------------------|----------------------|--------------|--------------|---------------|------------|---------|--|
| Cithaeronidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Edwards and Stiles 2011 |
| Trochanteridae_1 | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Gnaphosidae_1 | yes | yes | no | no | yes | no | no | N/A | Ibarra 1985; Yip and Rayor 2014; Pike et al. 2012; Perry and Roitberg 2006 |
| Gnaphosidae_2 | yes | yes | no | no | yes | no | no | N/A | Ibarra 1985; Yip and Rayor 2014; Pike et al. 2012; Perry and Roitberg 2006 |
| Gnaphosidae_3 | yes | yes | no | no | yes | no | no | N/A | Ibarra 1985; Yip and Rayor 2014; Pike et al. 2012; Perry and Roitberg 2006 |
| Molycrinae | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |
| Lamponidae | yes | yes | N/A | N/A | N/A | N/A | N/A | N/A | Platnick 2000 |
| Trochanteridae_2 | yes | N/A | N/A | N/A | N/A | N/A | N/A | N/A | |