Chapter 7
Social Recognition in the Arachnida

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Abstract More than 99 % of arachnid species are solitary, aggressive and often cannibalistic predators. A few species are social and cooperative, but they do not reach the level of eusociality found in some insects. Kin recognition is suggested to be a key feature for the evolution of cooperation and sociality and thus found predominantly in those few species. While kin recognition and social interactions are well investigated in spiders, these behaviours are understudied in other arachnid taxa. Nevertheless, social species are also known in the Acari, Pseudoscorpiones, Scorpiones, Opiliones and Amblypygi. Still, we have limited information on the adaptive value of social recognition in arachnids, how it is facilitated and maintained. While this field of research is still young, it has produced some encouraging results. This chapter reviews the knowns and the unknowns of social recognition mechanisms with respect to their importance for the evolution of arachnid sociality. We will particularly focus on kin recognition and kin discrimination. First, we shortly introduce the evolution of sociality in arachnids which provides the background for the understanding of the different recognition and discrimination mechanisms explained subsequently. Further, we illustrate the interspecific discrimination abilities of arachnids, and present the state of the art on intraspecific recognition and kin recognition in spiders and other arachnids. This chapter illustrates that various social recognition abilities and especially kin recognition exist in social but also non-social arachnids. These mechanisms allow different species to distinguish between familiar and foreign, or related and unrelated individuals, to either support or discriminate against them. In contrast to eusocial insects, the necessity of maintaining kin recognition abilities often appears to be obscure and highly context-dependent. Thus, a generalisation of its adaptive value in arachnids is not possible. There is some evidence for the concept of kin recognition facilitating the evolutionary transition from subsocial

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to permanently social living. However, kin recognition has not yet been demonstrated in permanently social species and is thus subject of ongoing research. It might have been lost during evolution due to the lack of encounters with unrelated individuals in permanent arachnid societies or replaced by direct benefits of cooperation. Finally, we discuss some research gaps and new approaches to improve the knowledge of the adaptive significance of kin recognition in arachnids.

Social Recognition in the Arachnida

Most arachnid species are solitary, aggressive and sometimes cannibalistic. Compared to insects, group living in these arthropods is an exception. More than 99 % of all species are solitary (Rayor and Taylor 2006). The level of sociality too, does not reach that of eusocial insects (Plateaux-Quènu and Roland 1997). Based on the less pronounced behavioural division of labour and the lack of a caste system, Whitehouse and Lubin (2005) refer to arachnid sociality as the ‘poor cousin of insect sociality’. Within the Arachnida, social interactions are well investigated in the Araneae but understudied in other taxa. Apart from spiders, social species are known in the Acari, Pseudoscorpiones, Scorpiones, Opiliones and Amblypygi. Some of the smaller groups, like Palpigradi and Ricinulei are very poorly known and thus a more general understanding of social aspects is not yet available (Rayor and Taylor 2006). Social recognition is a broad term that includes species recognition, and recognition of mating partners. As an example, courtship behaviour, which is extremely elaborate in many arachnids, has been suggested to function to identify species in a mate choice context and might therefore be considered a form of social recognition. In this chapter, we focus on the function of recognition in a social context including lose aggregations, group formations and cooperative behaviours. Our review on the social recognition abilities of arachnids will mainly focus on their impact on the evolution of group living and cooperation in this arthropod group.

For the evolution of cooperation and sociality, especially kin recognition is suggested to be a key feature (Hamilton 1964; Boomsma 2007), as documented in cooperatively breeding birds and mammals as well as the social insects (Griffin and West 2003). So far, we have still little information on whether arachnids show kin recognition, how kin recognition is facilitated, and the role of kin discrimination in social interactions. This chapter will review the state of the art of social recognition abilities in arachnids with a special focus on kin recognition, and we will thus start with a brief review of the evolution of sociality in these arthropods. In insects, sociality and social recognition have been extensively investigated and are discussed in this book. In particular, the importance and underlying mechanisms of kin recognition are well understood in insects, but their occurrence in arachnids is both astonishing and sometimes confusing, and the adaptive significance is often ambiguous. To date this field of research is still young and yet has produced some encouraging insights.

Sociality in Arachnids

Although rare in arachnids, group formation can be beneficial under certain conditions. It may help to reduce the risk of predation (e.g. Henschel 1998), increase foraging efficiency (e.g. Ward 1986) and increase the chance of finding a mating partner (e.g. Johannesen et al. 2007). As arachnids are predominantly predators, foraging motivation is considered to be a significant driving force that explains the advantage of group living in these animals (Fig. 7.1) (Brach 1975; Nentwig 1985; Wickler and Seibt 1993; Majer et al. 2013a). In groups, arachnids are able to better monopolise locally rich food sources; and larger prey animals or a greater number of items may be better overwhelmed when attacked communally. The size of prey can be between four times larger in some Pseudoscorpions (Tizo-Pedroso and Del-Claro 2007) to 16 times larger in some spiders (Ward 1986) compared to the weight of a single individual. Powers and Avilés (2007) found that the average size of prey items rather than the amount of prey biomass positively correlates with the level of sociality in *Anelosimus* spiders. Such coherency may be particularly important for juveniles as the group foraging mode increases survival and facilitates a reasonably quick development. Food availability is likely to facilitate group cohesion and tolerance to other individuals in close proximity. The richer a food source, the stronger is the bonding of groups mediated by intraspecific tolerance (Gundermann et al. 1993; Schneider 1995; Kim 2000). In contrast, under low food conditions, competition over prey (Bilde et al. 2007) or increased cannibalism (Bilde and Lubin 2001) may counteract group living. Consequently, cooperation has been found in environments with temporally stable prey abundances such as the tropics (Yip et al. 2008; Del-Claro and Tizo-Pedroso 2009; Majer et al. 2013b). On the other hand, lower prey availability or greater prey size may render cooperation more necessary.

The pathways of group formation in arachnids have been intensively investigated in spiders, and the evolutionary concepts have often been adopted for other taxa. One of the most important prerequisites for social bonding is tolerance of other individuals. As predators, arachnids usually behave aggressively not only towards potential prey but also towards conspecifics that may represent competitors as well as potential prey. However, many species of spiders, scorpions and pseudoscorpions exhibit maternal care, and the brood remain in close proximity to the mother. Accordingly, the juveniles show lower intraspecific aggression levels. Overcoming aggression or extending juvenile tolerance respectively, is crucial for moving on to the next stage, interaction (Kullmann 1968), which facilitates the formation of groups. So, intraspecific tolerance allows the development of gregarity as one of the simplest forms of social interactions. Loose short-term aggregations to share a shelter, to exploit a resource or to protect themselves against predators are known for several arachnids, such as harvestmen (Chelini et al. 2012), scorpions (Polis and Lourenço 1986), mites (Mailleux et al. 2011) and spiders (Buskirk 1981). The most advanced level of social living is cooperation, characterised by individuals working together to accomplish a certain task to obtain individual fitness benefits (Whitehouse and Lubin 2005). Group tasks may comprise the collective construction of retreats, brood chambers and capture webs (in spiders), prey capture, communal feeding and brood care

Fig. 7.1 A group of six *Stegodyphus dumicola* females attacking grasshopper caught in the capture web of the colony. (*photo* André Walter)

(Kullmann 1972; Lubin and Bilde 2007). However, even the most advanced social species still do not reach the eusocial level of insects with strict worker castes and complex social coordination (Lubin and Bilde 2007), although recent studies indicate the presence of basic forms of division of labour at least in some social arachnids (Grinsted et al. 2013; Settepani et al. 2013; Wright et al. 2014).

Generally, the type and organization of social interactions differ among group living arachnid species. The presence or absence of cooperation among group members, and the duration of the social and cooperative stage, is crucial for the distinction of different types of sociality. Species with close-together living but typically without cooperation and allo-maternal care are ‘gregarious’ or ‘colonial’, and also some ‘kleptoparasitic’ species fall into this category that we refer to as ‘colonial’ (Agnarsson 2002; Bilde and Lubin 2011). Their group formation is the result of aggregations of mainly unrelated individuals, often around a rich food source, but they remain solitary in their behaviour and do not cooperate with conspecifics (Uetz and Hieber 1997). Individuals of ‘subsocial’ and ‘social’ species show cooperation, and groups originate from family bonding. While subsocial species form groups only periodically, the social species live in permanent colonies (Lubin and Bilde 2007; Bilde and Lubin 2011). In the subsocial state, offspring of a single mother form groups to cooperate temporarily, but dispersal occurs before mating and most species adopt solitary living. Periodic social living is facilitated by the extended maternal care, hence the term subsocial behaviour. Social species build permanent nests, sometimes with overlapping generations, and show reproductive skew and allo-maternal care. They can be compared with cooperative breeders (like in birds and mammals) that have helpers at the nest that help rearing the offspring.

Evolution of Sociality in Arachnids

The evolutionary progression to sociality proposes two major scenarios that are generally accepted to explain the appearance of group living in Arachnids, the ‘parasocial route’ and the ‘subsocial route’ (Avilés 1997; Plateaux-Quènu et al. 1997; Schneider 2002). Both scenarios have led to different degrees of sociality reaching from colonial, over subsocial to permanent cooperative species (Whitehouse and Lubin 2005; Lubin and Bilde 2007).

The ‘parasocial route’ describes the evolution of group living via aggregation of individuals of otherwise solitarily living species (Wickler and Seibt 1993). In colonial spiders, for example, colonies of webs can be found clustered around a rich food source in order to exploit it more efficiently. The spiders use common frame threads, but each individual maintains its own webs and feeds solitarily, and conspecifics may not be accepted within individual webs (Jackson 1982; Bowden and Jackson 1988). Aggregations are associated with close contact among individuals. Thus, this scenario requires the overcoming of intraspecific aggression and the abandonment of territoriality. In many harvestmen, pseudoscorpions and scorpions individuals temporarily aggregate and tolerate each other to seek shelter or to exploit a rich resource in a spatially limited habitat, but show no indication of cooperation (Rayor and Taylor 2006), which is the key feature of permanently social living. The ‘parasocial route’ may also explain the evolution of kleptoparasitism, where, for example, spider species aggregate in webs of their hosts to feed on prey remains (Agnarsson 2002). However, the ‘parasocial route’ is also associated with the risk of aggressions as a result of competition around a food source, and is therefore unlikely to explain the occurrence of cooperative sociality in arachnids.

The ‘subsocial route’ pathway describes the evolution of sociality via extended maternal care. Here, related offspring stay together over a period of time after hatching and display intra-group tolerance. Ultimately, permanent sociality is achieved by the complete elimination of pre-mating dispersal. Maternal care is widespread amongst arachnids (Yip and Rayor 2014) and it seems likely that extended maternal care and the resulting formation of family sibling groups is a pre-condition for sociality to evolve (Lubin and Bilde 2007). For the maintenance of group cohesion, juvenile dispersal has to be delayed to prolong the time of intraspecific interaction, mainly between mother and offspring, to allow selection to act on behaviours that facilitate further social evolution. In many arachnid species the mother individual cares for the young by protecting them against predators, building a sheltering nest, by providing them with captured prey, by feeding them through regurgitation of nutritious fluids or by scarifying herself to the offspring to maximize maternal investment (Lubin and Bilde 2007; Del-Claro and Tizo-Pedroso 2009). If juveniles stay together for several instars to cooperate beyond the mother's death, the criterion of a subsocial relation is fulfilled (cf. definition in Agnarsson et al. 2006). In an even narrower sense, extended maternal care might be already considered as a subsocial behaviour. However, at the same time the pre-mating dispersal drive of the young also needs to be suppressed to ensure group cohesion over a certain time (Gundermann et al. 1993; Schneider 1995; Avilés 1997). Usually, juveniles live together until competition for food triggers dispersal, or until they have reached a species-specific body mass or size to disperse. Wickler and Seibt (1993) suggested a more specific term for the 'subsocial route', referring to a 'sibling route' in the evolution of sociality. The evolution of permanent sociality through cooperation among siblings would be favoured by inclusive fitness benefits and thus kin selection (Hamilton 1964; Maynard Smith 1964). Especially in a transitional stage and if individuals encounter conspecifics of varying relatedness, this requires recognition mechanisms to direct cooperative actions towards kin.

Interspecific Discrimination in Arachnids

Arachnid species that show social behaviour are characterised by high intra- and often interspecific tolerance when forming groups (spiders: Seibt and Wickler 1987/scorpions: Shivashankar 1994; Lourenço and Cloudsley-Thompson 2011/pseudoscorpions: Weygoldt 1969; Del-Claro and Tizo-Pedroso 2009/harvestmen: Machado and Macías-Ordoñez 2007; Chelini et al. 2012/mites, Mori and Saito 2006; Mailleux et al. 2011; Strodl and Schausberger 2012b). Unless there is indiscriminate tolerance of any foreign individual, these species must have developed recognition abilities to discriminate acceptable group members from those that will be refused. Given ageneral advantage of group living, species may choose to associate with congeners, unrelated conspecifics or only with siblings. The latter is of particular interest in subsocial and social arachnids.

The most basic level of recognition is that of dead and alive. Brach (1977) found in the social spider *Anelosimus studiosus* (Theridiidae) that any conspecific individual that has joined the colony is considered as co-operator as long as it is alive. Dead spiders will be treated as prey, an action that of course may also be considered as sanitation behaviour to keep the communal nest healthy. The distinction on the next higher level refers to the genus or species level. Individuals that intrude into a colony but belong to a completely different taxon may potentially represent predators or kleptoparasites. In *Stegodyphus sarasinorum* (Erisidae), Kullmann (1972) noticed an interesting recognition mechanism in which individuals of the species recognise erisid-typical (spider family Erisidae) body features but without having the ability to discriminate between different species or conspecifics. Consequently, Kullmann (1972) showed in manipulative experiments that an association between different species is possible through a reduced interspecific aggression level. The recognition mechanism has been suggested to be based on chemosensitive perception via pheromones (Kullmann 1972). A similar congeneric acceptance has also been revealed for two social *Stegodyphus* species (Seibt and Wickler 1988). The interspecific acceptance is high enough to even allow the formation of mixed species groups that perfectly cooperate. Experimentally brought together in the lab, *Stegodyphus mimosarum* (Fig. 7.2) and *Stegodyphus dumicola* cooperatively build webs and forage (Seibt and Wickler 1988). Later Grinsted et al. (2012) found a similar behaviour realised in the wild. Two *Chikunia* species (Araneae; Theridiidae) were found to form mixed colonies. These spiders do not forage together, but lab experiments suggest that there might be interspecific brood care as females of one species adopt the young of the other (Grinsted et al. 2012). Other examples on congeneric group member acceptance can be found in social and subsocial species of the theridiid spider genus *Anelosimus* (Samuk and Avilés 2013), or in gregarious species of the harvestmen genus *Serracutisoma* (Chelini et al. 2012). However, in the latter example individuals show a clear preference to associate with conspecifics indicating that species discrimination is also present.

The fact that many group living species tolerate congeners may indicate that the evolution of social interactions via the para-social route has started with a general lowering of aggression to gain direct benefits of association. However, permanent sociality and cooperation in arachnids appear to only evolve through the sub-social route based on kin selected benefits (Anthony 2003; Lubin and Bilde 2007). Hence, tolerance alone is not a mean of inter- and intra-specific cooperation. Tolerance towards conspecifics and low interspecific aggression may, however, play a significant role in the evolution of kleptoparasitism. Agnarsson (2002) noted that these behavioural patterns can be found in kleptoparasitic *Argyrodes*—species (Theridiidae). In social species, the tolerance is mutual between juveniles and the larger mother individual. Usually, a larger animal might be considered as a predator. Therefore, not trying to escape when being in its close proximity is not self-evident. Small *Argyrodes* spiders of different species had to overcome this barrier to enter the host spider's web that is always much larger in body size (Agnarsson 2002). As more than one *Argyrodes* individual and sometimes more species occupy a host web, additional intraspecific tolerance is essential to avoid competitive fights that may alert the host spider. Hence, it is reasonable to assume that at least in the family Theridiidae, which comprises social and as well as kleptoparasitic species, the same tolerance-mechanisms may represent the evolutionary origin for both lifestyles.

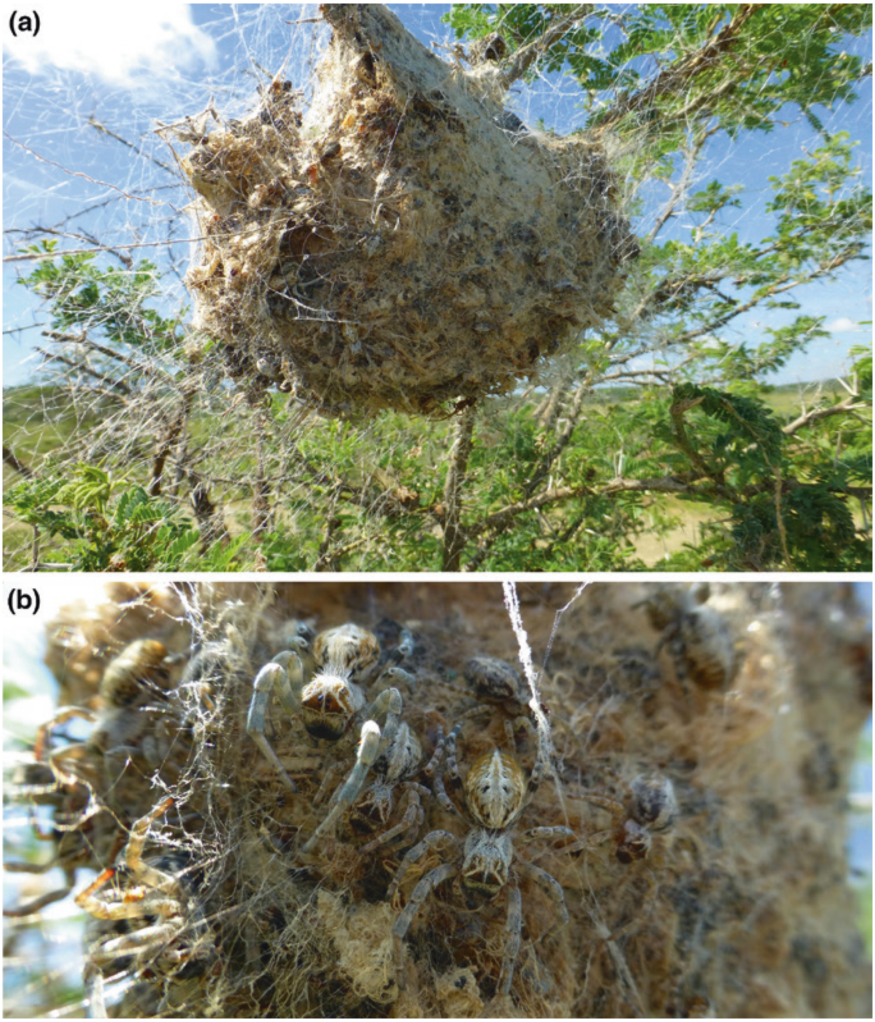

Fig. 7.2 A nest of social *Stegodyphus dumicola* spiders (Erisidae) in Weenen Nature Reserve/ South Africa. **a** total view, **b** close up. (*Photos* André Walter)

The cues used to identify members of the same species are various and not always fully understood. Both tactile (Wilson 1971; Brach 1975) and chemical stimuli (Kullmann 1972) have been described as effective discrimination cues used in different species. In particular, pheromones play an important role for arachnid species recognition but also for intraspecific attraction to form groups (spiders: Seibt and Wickler 1988; Evans and Main 1993; Trabalon and Assi-Bessékon 2008/ whip spiders: Hebets and Chapman 2000; Walsh and Rayor 2008/mites: Sato et al. 2003; Mailleux et al. 2011; Clotuche et al. 2012). In some social spider species, pheromones deposited on silk will attract individuals to form a group or to join an already established one (*Diaea socialis*, Evans and Main 1993; *S. mimosarum* and *S. dumicola*, Seibt and Wickler 1988). Chemical cues may also be used by particular conspecifics in specific contexts or functions. Females of *D. socialis* are not attracted to juvenile silk (Evans and Main 1993), and the silk of incubating females of the subsocial *Coelotes terrestris* (Agelenidae) attracts mated females but repels virgins (Trabalon and Assi-Bessekon 2008).

It may not surprise that species recognition is widespread also among arachnids as it is an important mechanism to ensure intraspecific matings. Its role for composing groups with conspecifics only is nevertheless still understudied. Species recognition may facilitate the evolution of cooperation through behavioural similarities among individuals of the same species. The nature of interactions among conspecifics may depend on familiarity, developmental stage, sex, and, as shown later, relatedness. For example, in the predaceous mite *Phytoseiulus persimilis* larvae stay together in groups until they moult into protonymphs. These larvae show a preference for grouping with individuals that they are familiar with because they were previously exposed to the same environment, whereas other factors like kinship do not significantly influence aggregation behaviour (Strodl and Schausberger 2012a). Yet another form of discrimination based on sex can be found in the social theridiid spider *A. studiosus*. Conspecific intruders are accepted in the colony, but this does not account for the scenario of a resident adult female encountering another immigrant adult female (Brach 1977). The resulting fight can be considered as competition over a nest and foraging site that is chosen by the resident female to raise her own offspring. The developmental stage may additionally be an important factor to trigger either aggression or cooperative behaviour (e.g. Yip et al. 2012). It is possible that intruding subadult individuals benefit the colony for example by increasing the probability of survival, whereas adult conspecific females are detrimental through the increased competition between offspring of the two families.

In *S. mimosarum* and *S. dumicola* the mother will sooner or later be eaten by her young spiderlings (‘matriphagy’). These spiders are semelparous and although not unambiguously proven yet, it is likely that mothers signal to the young to consume her at a certain point in time after regurgitation feeding has started. However, at this stage juvenile spiders not only eat their mother but would also attack any other female of their mother’s age (thus also called ‘gerontophagy’ by Seibt and Wickler 1987). In the subsocial spider *Stegodyphus lineatus* the mother feeds her young after hatching but also provides food to unrelated conspecific young. She only does this, however, if they are within the same instar as her own offspring (Schneider 2002). This maternal behaviour suggests that physiological stage and not discrimination per se is involved in this extreme form of maternal care. Nursing females of the subsocial agelenid spider *C. terrestris* are tolerant to related and unrelated juvenile individuals, but when experimentally confronted with young in the pre-laying or incubating state they would occasionally attack them (Assi-Bessékon and Horel 1996). Cuticular chemical cues have been suggested to mediate this discrimination mechanism (Assi-Bessékon 1997).

With permanent sociality where colonies persist over several years, some species show complete overlapping of generations (e.g. *Anelosimus*) whereas others show partial overlap (e.g. *Stegodyphus*). Permanent social group formation is not only favoured by higher protection and efficiency of foraging, but also by indirect fitness benefits mediated by reproductive skew and allo-maternal brood care that increase survival and reproduction at the colony level (Grinsted and Bilde 2013). When it comes to reproduction, inclusive fitness theory (Hamilton 1964) predicts that cooperative breeding should evolve among related individuals. Intraspecifically, further discrimination mechanisms may be necessary to optimise this level of cooperation. If cooperation evolves from family groups, kin recognition and kin discrimination may not evolve, simply because interactions among non-kin are rare. In this case, either 'familiarity' by recognition of nest mates, or a simple rule stating 'cooperate with nest mates' will effectively have the same evolutionary outcome as kin-mediated interactions (Griffin and West 2003; Schneider and Bilde 2008).

Intraspecific Discrimination and Kin Recognition

Kin recognition describes mechanisms that may lead to differential treatment of conspecifics based on genetic relatedness (Sherman et al. 1997). Following kin selection theory, kin directed cooperation is favoured by inclusive fitness benefits, i.e. the sum of own direct fitness and indirect fitness of relatives with whom they share genes identical by descent (Hamilton 1964; Maynard Smith 1964). Cooperation is expected to evolve when individuals gain higher inclusive fitness by helping to raise offspring of close relatives than they would through own reproduction. This coherency also known as 'Hamilton's rule' applies for many social insect systems as well as cooperatively breeding vertebrates (Boomsma 2007; Griffin and West 2003). It follows that mechanisms that allow recognising kin and directing help towards them will be favoured by selection. Kin recognition has been documented in a number of subsocial arachnids (see below) and appears to play a role in the evolution of cooperation. Kin recognition may also be important in solitary arachnids that are prone to early life competition or cannibalism, as it occurs in some predatory mites (Schausberger 2007; Strodl and Schausberger 2012a, b). As many taxonomic groups have not been studied (Table 7.1), general conclusions about the occurrence and adaptive significance of kin recognition cannot be drawn. However, based on the present data its benefits seem to be unequally distributed across the taxon and often not easy to reveal (Evans 1999). It is important to note that the apparent lack of kin discrimination does not necessarily imply that this trait is absent; it may simply not be in use in relation to the behaviours under investigation. Likewise, the ability to recognise kin does not necessarily imply that nepotism through kin-directed helping takes place (cf. Waldman et al. 1988). For example, in subsocial *Stegodyphus* spiders kin recognition mechanisms have been found (see below) but behavioural differentiations between related and unrelated individuals are not always noticeable (Schneider 1996). Finally, it is important to distinguish between genetic kin discrimination and familiarity, where discrimination is based upon recognition of individuals and not their genetic relatedness. While the evolutionary outcome of these two modes of recognition could be the same, they represent fundamentally different mechanisms of recognition (Schneider and Bilde 2008). Some studies putatively reveal kin discrimination although the control for a distinction to familiarity may have been lacking. To show 'true' kin recognition, both genetic relatedness and familiarity must be controlled as independent factors (see below). For simplification in the following section we will refer to the term 'kin recognition' even if a genetic basis has not been proven. As the occurrence and relative importance of kin recognition mechanisms differ among taxa, we will review spiders and other arachnids separately in the following sections.

Sociality and Kin Recognition in Non-spider Arachnids

The degree of sociality in non-spider taxa varies greatly. While in harvestmen only gregarious behaviours are known (Chelini et al. 2012), some scorpion species can be regarded as subsocial as they show extended maternal care (Lourenço and Cloudsley-Thompson 2011). Mothers of the buthid scorpion *Tityus neblina* care for their young by protecting them and providing them with food. Other (non-buthid) species build communal nests, hunt cooperatively and feed communally (Shivashankar 1994). However, these associations are only temporary, and permanent sociality is not known for this arachnid group (Lourenço and Cloudsley-Thompson 2011). Kin recognition abilities may be present in scorpions. Mahsberg (1990) found in choice experiments that lab-raised juveniles of the subsocial scorpion *Pandinus imperator* prefer to associate with their own mother rather than with an unrelated female. Yet aggression against non-kin individuals has been reported to be very low (Mahsberg 1990). The result of the study of Mahsberg (1990), however, can also be explained by familiarity (cf. categories in Table 7.1) because prior to the experiments the juvenile scorpions stayed with their mother until the second instar. This gave them time to familiarise, and the outcome of the choice test may not necessarily mirror a preference based on genetic relatedness. In pseudoscorpions the situation seems very similar. Also here some species show subsocial behaviours that include nest cohabitation and food share until the offspring disperses (Del-Claro and Tizo-Pedroso 2009). Moreover, species of the genus *Paratemnoides* perform cooperative parental care, and in *P. nidificator* even a basic form of an age dependent division of labour has been suggested (Tizo-Pedroso and Del-Claro 2011). Kin recognition, however, has not yet been described. The only example of true kin recognition apart from spiders and mites (see below) comes from whip spiders (Amblypygi). Again, the evolutionary origin of their social interaction is an extension of maternal care (Rayor and Taylor 2006). For example, juveniles of *Phrynus marginemaculatus* and *Damon*

Table 7.1 The Knowns and unknowns about kin and nest mate recognition in arachnids

Affected traits	Taxon					
	Pseudoscorpiones	Scorpiones	Acari	Opiliones	Amblypygi	Araneae
Recognition based on familiarity						
Increased investigation	x	x	*Phytoseiulus persimilis*[17]	x	x	*Delena cancerides*[20]
Preferred association	x	*Pandinus imperator*[7]	x	x	x	Anelosimus eximius[8*] Stegodyphus lineatus[6]
Preferrential cannibalism	x	x	*Phytoseiulus persimilis*[12,13,14]	x	x	*Delena cancerides*[1*,10] *Diaea ergandros*[4] *Hogna helluo*[9] *Stegodyphus lineatus*[2]
Improved defence	x	x	*Phytoseiulus persimilis*[18]	x	x	x
Improved feeding efficiency through association with kin	x	x	*Phytoseiulus persimilis*[17,21]	x	x	*Stegodyphus lineatus*[15]
Recognition based on genetic cues						
Preferred association	x	x	x	x	*Damon diadema*[19]	x
Preferrential oviposition	x	x	*Iphiseius degenerans*[5]	x	x	x
Preferrential maternal feeding	x	x	x	x	x	*Diaea ergandros*[3]
Preferrential cannibalism	x	x	*Phytoseiulus persimilis*[12,13,14] *Phytoseiulus macropilis*[14]	x	*Damon diadema*[19]	x
Improved feeding efficiency through association with kin	x	x	x	x	x	*Stegodyphus lineatus*[15] *Stegodyphus tentoriicola*[11]

Several studies found individual recognition abilities without unravelling whether it is based on genetic relatedness or familiarity. We thus list the literature in two categories of 'kin recognition'. However, it might be shown in future investigations that some species assigned to 'familiarity' may in fact also possess kin recognition based on genetically based cues

Studies we indicated with "*" refer to nestmate recognition not specifically revealing or addressing genetic relatedness

References: (1) Beavis et al. (2007), (2) Bilde and Lubin (2001), (3) Evans (1998), (4) Evans (1999), (5) Faraji et al. (2000), (6) Johannesen and Lubin (2001), (7) Mahsberg (1990), (8) Mailleux et al. (2008), (9) Roberts et al. (2003), (10) Rowell and Avilés (1995), (11) Ruch et al. (2009), (12) Schausberger (2005), (13) Schausberger (2007), (14) Schausberger and Croft (2001), (15) Schneider (1996), (16) Schneider and Bilde (2008), (17) Strodl and Schausberger (2012a), (18) Strodl and Schausberger (2012b), (19) Walsh and Rayor (2008), (20) Yip et al. (2009), (21) Zach et al. (2012)

diadema stay with their mother for at least one year until they become solitary. In *D. diadema,* mothers and her offspring further show active aggregation under increased predation risk (Rayor and Taylor 2006). As the mentioned species show no cooperative prey capture or food share, the function of group living is most likely protection. Despite the lack of cooperation, kin recognition has been found in immature individuals of *D. diadema* (Walsh and Rayor 2008). In Y-maze choice tests, Walsh and Rayor (2008) showed that immature individuals are able to recognise their mother. Recognition is probably based on olfactory cues, as amblypygids are very sensitive to odours (Hebets and Chapman 2000), and tactile stimuli, as they use their 'whips' (first pair of legs) to physically contact conspecifics (Rayor and Taylor 2006). One hypothesis for the significance of immature kin recognition is that remembrance of siblings in the adult stage may serve to avoid serious injuries during fight, because adult whip spiders behave aggressively when they encounter potential conspecific competitors (Walsh and Rayor 2008).

The large arachnid group of mites (Acari) is trophically diverse, comprising vegetarian, predaceous and parasitic specialists. The sociality levels cover the whole range from solitary to subsocial and permanently social species that build large colonies with overlapping generations and even bi-parental brood care (Sato et al. 2003). Kin recognition has been revealed for various species but has not (yet) been found in the group of highly social spider mites. The advantages of group living in mites include reduction of evaporative water loss (Glass et al. 1998), increased foraging efficiency (Strodl and Schausberger 2012a) and increased survival by cooperative defence against predators (Mori and Saito 2005; Strodl and Schausberger 2012b). The latter is particularly evident for species that build common nests (Mori and Saito 2004, 2005). Even inherently solitary species, like the house dust mite *Dermatophagoides pteronyssimus*, sometimes form groups. When certain individuals start to migrate to new food patches they lay trails of chemical cues that attract conspecifics to follow (Mailleux et al. 2011). Hence, the migration becomes a collective phenomenon. Moving in a group may help to reduce dehydration risk, but interactions between individuals are lacking (Mailleux et al. 2011). Non-social predatory mites naturally show no expression of cooperation, but some species possess kin recognition abilities. Females of *Iphiseius degenerans* oviposit preferably next to eggs laid by related females rather than unrelated ones (Faraji et al. 2000). This behaviour is suggested to reduce the risk of kin cannibalism among juveniles once they will have hatched, as young are less likely to cannibalize relatives. In *P. persimilis* and *P. macropilis,* adult females tend to prey upon juvenile conspecifics with a significant preference for unrelated individuals (Schausberger and Croft 2001). Both species show no social behaviours and yet the authors discuss the adaptive significance of their kin discrimination abilities in context of inclusive fitness theory. In the case of a recognition error, females would experience a loss of inclusive fitness by eating related individuals (Schausberger and Croft 2001). Moreover, reducing the number of unrelated offspring by increased predation will finally relieve the young from intraspecific competition for food. This particular example refers to a recognition mechanism that might be the direct result of kin selected behaviours, however, Schausberger

(2007) later revealed that in *P. persimilis* kin recognition is an amazingly complex, context-dependent process. While these mites use genetically determined recognition cues, discrimination is nevertheless based on familiarity. An association early in life will reduce cannibalistic behaviours against familiar individuals in later juvenile stages, irrespective of whether they are kin or non-kin. Staying in a group of familiar individuals increases foraging efficiency (Strodl and Schausberger 2012a; Zach et al. 2012) and reduces response time to predatory attacks (Strodl and Schausberger 2012b), which is suggested to be mediated by the reduced time needed for the assessment of conspecifics (Strodl and Schausberger 2012a, b). The advantage of a familiarity-based recognition mode in *P. persimilis* is that it allows mothers to lay eggs next to clutches of unrelated females, and still juvenile cannibalism after hatching remains low (Schausberger 2007). Interestingly, the same species is also capable of 'true' kin recognition based on phenotype matching. Although the cannibalism rate is generally higher towards unfamiliar individuals, Schausberger (2007) demonstrated in a choice experiment that under food deprivation protonymphs prefer to cannibalise sibling larvae over non-sibs irrespective of the degree of familiarity. This latter behaviour is suggested to represent a selfish action to avoid competition of related alleles and to increase direct fitness (Schausberger 2007). Nevertheless, those benefits must be enormous for kin cannibalism to be adaptive given the cost of losing inclusive fitness, and may include an inbreeding avoidance strategy. Alternatively, kin cannibalism may also result from preferential association with kin and thus a by-product occurrence of early cannibalism on related individuals without indicating a true preference (see also Schausberger 2005). The example of predatory mites nicely illustrates that kin recognition also occurs in non-social species and that both processes, kin recognition based on genetic relatedness and familiarity, appear to be important in social interactions among various mite species.

Spider mites are considered as pest on crops (Saito 1987) yet showing high level of sociality. Apart from building permanent nests with overlapping generations, cooperation in nest construction, nest sanitation (Sato et al. 2003) and nest defence (Mori and Saito 2005) some species even perform bi-parental brood care (Saito 1987) which might be related to their genomic structure. While arachnids are typically diploid, some social spider mites are characterised by haplodiploidy which adds a particularly interesting aspect to the function of kin recognition. Similar to eusocial hymenopteran insects females of these mites produce haploid males (from unfertilised eggs) and diploid females. Despite the fact that in social spider mites no reproductive division of labour exists (Mori and Saito 2006), colonies are often founded by single females. The within-colony relatedness can be high, because a highly female biased sex ratio of the offspring has also been reported [e.g. *Tetranychus urticae* and *Schizotetranychus celaris*, Saito (1987); *Stigmaeopsis longus* and *S. miscanthi*, Sato and Saito (2007)]. Through mother-son matings the relatedness within a colony can be further increased, as it is the case in *S. celaris* (Acari, Tetranychidae). This mating behaviour may explain the unusual occurrence of paternal brood care, since in this inbreeding scenario the offspring has a much higher relatedness to the father than they would have if the father mated with a female from a foreign colony (Saito 1986, 1987). Kin recognition could be beneficial in order to maintain this male-offspring-relatedness by preferential matings with related females, but it has not been revealed for any permanently social mite species so far. Moreover, despite the complexity of social behaviours and a haplo-diploid system, Mori and Saito (2006) could neither find division of labour nor casts in *Schizotetranychus*.

Kin Recognition in Subsocial Spiders

Kin recognition in spiders is tightly linked with sociality and has not yet been found in solitary species (excluding species with extended maternal care as a form of sub-social behaviour). This might well be an artefact of a biased investigation, but it may also underpin the importance of kin recognition to facilitate the evolution of sociality in these animals. In spiders, kin recognition mechanisms are subtle and comprise a number of specific behaviours that are often highly context-dependent (Yip and Rayor 2014). Those mechanisms may be used to direct help towards related individuals in social groups or to discriminate against foreigners. *Delena cancerides*, a social huntsman species of the family Sparassidae, has reached a unique discrimination level. Colonies in this species may comprise up to 300 individuals that form social nests under the bark of trees, and in contrast to all other social arachnids, they behave aggressively towards individuals from foreign colonies (Rowell and Avilés 1995). Chemical cues may be used by the individually hunting spiders to find back to their own colonies. Those cues would also mark the home nest, and with it all inhabiting spiders, and may thus be used for nest mate recognition (see Rowell and Avilés 1995). In the permanently social *Anelosimus eximius* (Theridiidae), Pasquet et al. (1997) showed that volatile and non-volatile cuticular substances vary considerably among colonies. However, introduction of individuals from foreign colonies with different ‘odours’ did not appear to elicit measurable behavioural changes like increased aggression. This result, that differs from *D. cancerides*, may be related to the rather static nature of group living in *A. eximius*, as there is almost no individual exchange between colonies and thus direct competition among colonies over resources is rather weak (Pasquet et al. 1997). Moreover, social spiders tend to include foreigners in their colony because of benefits for survival, and selection against such inclusion is low despite the fact that large colonies may also experience higher intraspecific competition. Accordingly, it has been shown in *A. eximius* as well as in the social *S. dumicola* (Erisidae) that larger nests survive better than smaller ones (Avilés and Tufiño 1998; Bilde et al. 2007). In *D. cancerides* individuals are free hunting and more mobile, and therefore colonies are more often faced with wandering immigrants (Yip et al. 2012). They may be forced to actively maintain colony integrity, especially if colony retreats represent a limited resource (Yip et al. 2009). Interestingly, although sociality in *D. cancerides* is also suggested to originate from extended maternal care, colonies also comprise a substantial proportion of unrelated individuals. Thus, the pronounced discrimination against foreigners is based on both kin and non-kin nest mate recognition (Rowell and Avilés 1995). Is has subsequently been shown that true kin recognition exists in this species (Beavis et al. 2007). For a long time, it was unknown how the high level of intolerance towards immigration of unrelated individuals could result in mixed colony compositions, which is important to maintain outbreeding opportunities. Beavis et al. (2007) eventually found that adult females that founded a colony are reasonable tolerant towards juveniles with carapace width of less than 6 mm (see also Yip et al. 2009). Thus, juvenile dispersal may be the only way in this species to join groups of unrelated spiders and to maintain an outbred population structure (Yip et al. 2012).

That true distinction between kin and non-kin might be of adaptive significance in arachnids was shown in studies on subsocial *S. lineatus* (Schneider 1996; Bilde and Lubin 2001; Schneider and Bilde 2008). Under low food conditions these spiders show increased cannibalism in groups of unrelated individuals, which has been discussed in context of inclusive fitness maximisation (Bilde and Lubin 2001). Other studies revealed that subsocial *S. lineatus* also perform better when they forage in groups of siblings instead of mixed associations (Schneider 1996; Schneider and Bilde 2008). Kin groups fed more efficiently by extracting more food from the prey and grew at a higher rate. Schneider and Bilde (2008) used cross fostering experiments to prove that genetic relatedness and not familiarity among colony members improved the performance in *S. lineatus*. This study did not detect the mechanisms of kin recognition, but it was later shown that kin recognition in *S. lineatus* may be mediated by cuticle hydrocarbons (Grinsted et al. 2011). The behavioural or physiological mechanisms of kin discrimination in communal feeding events, however, are still unknown. Perhaps, these spiders invest differentially in digestive enzyme production and/or contribution to the extra-oral digestion when foraging with either kin or non-kin. Beyond an 'optimal' group size, further individuals that join will increase competition over food and the incentive for cheating (Whitehouse and Lubin 2005). Accordingly, Ruch et al. (2009) found that feeding efficiency decreases with increasing group size in subsocial *Stegodyphus tentoriicola*. This effect, however, is less pronounced in sibling groups and thus indicates a potential advantage of discriminating against non-kin when forming groups. The different feeding efficiency might be related to a dissimilar investment in releasing digestive enzymes (Ruch et al. 2009). As the production of digestive fluids is costly (Secor 2003) the motivation not to contribute own enzymes, and thus to cheat, may be enhanced in mixed groups. Nevertheless, cooperation can be maintained despite cheating if a single individual is unlikely to successfully monopolise a resource (Lubin and Bilde 2007). However, cheating creates a social dilemma as related individuals lose indirect fitness benefits (Schneider and Bilde 2008).

Cooperation may conflict with competition among members of a colony, for example over the best feeding-positions, the greatest share of captured prey items, or mating partners etc. Competition increases with increasing group size, which leads to a reduction in per capita fitness (Bilde et al. 2007). Under these conditions cheating becomes a tempting strategy (Lubin and Bilde 2007). Individuals may decide not to contribute to prey capture or web construction although taking advantage of both, or they may not contribute in producing and releasing digestive fluids while feeding communally. Following the theory of 'the tragedy of the commons' (Hardin 1968) selfish actions reduce the benefits of cooperation for other group members. Kin recognition may help to reduce negative effects of selfish actions because interacting with related individuals increases the cost of cheating by reducing inclusive fitness (Schneider and Bilde 2008). A preference for associating with kin may reduce the level of cheating and thus underpins the significance of kin recognition for the evolution of cooperation and the transition to permanently social spider societies (Lubin and Bilde 2007).

In the thomisid subsocial spider *Diaea ergandros*, Evans (1999) showed that the performance of sibling groups does not significantly differ from groups of unrelated individuals in the adult stage. Juveniles, however, contribute more to nest construction when cooperating with siblings, and if unfavourable conditions causes the colony to starve, cannibalism spreads and spiders then prefer to eat non-sibs first (Evans 1999). This would conform to kin-selection theory. However, the discrimination modes turned out to be complex. Starving subadult females would prefer to cannibalise foreign females but related males. This differential response was attributed to facilitation of outbreeding opportunities (Evans 1999; see also Johannesen and Lubin 1999).

Kin Recognition and Permanent Sociality in Spiders

It is evident that kin recognition is favoured by inclusive fitness benefits, and most likely kin cooperation plays a role in the transition to permanent sociality in spiders. So far, kin recognition has not been found in permanently social spiders. Perhaps, once permanent sociality has evolved, there may be additional selective forces that maintain cooperation. For example, high and predictable genetic relatedness among group members may relax selection for maintaining kin recognition (Lubin and Bilde 2007; Yip and Rayor 2014). Also, mutualistic benefits of cooperation (see Kokko et al. 2001) and infrequent encounters with competing groups would reduce the need for a kin recognition system (Waldman 1988). These conditions characterise permanently social spiders, that are severely inbred with low intra-colony genetic variation (Lubin and Bilde 2007), and group augmentation increases colony survival (Avilés and Tufiño 1998; Bilde et al. 2007). Indeed, the scarce evidence for kin discrimination and nepotism in permanently social species support relaxed selection for these traits, and it is therefore possible that they have been lost with the transition from subsocial to permanently social living (Lubin and Bilde 2007; Berger-Tal et al. 2015). This observation underlines that kin recognition in spiders and other arachnids is not an obligate prerequisite for the maintenance of group living and cooperation. However, social spiders may well benefit from kin selected traits that led to their level of cooperation. If they gain both inclusive fitness from allo-maternal care, and direct fitness from increased survival of larger groups, this is sufficient to explain the maintenance of cooperation. An alternative explanation, the principle of reciprocity (Axelrod and Hamilton 1981), requires score-keeping, individual recognition and repeated interactions amongst individuals. While this could in principle happen, by-product mutualism (Eberle and Kappeler 2008) would be more likely to explain direct benefits of cooperation in spiders.

Kin Recognition Cues

Kin recognition has been demonstrated in several spider species, whereas we have yet to understand the actual underlying recognition mechanisms. As shown above, for interspecific recognition mechanisms, spiders use tactile chemical cues to regulate their interactions. Chemicals deposited on silk are well known to serve as effective cues (Seibt and Wickler 1988; Evans and Main 1993), but have not yet been revealed to play a role in kin recognition. For example, *S. lineatus* is able to recognise the silk of its own species, but individuals do not show any preference for the silk of kin or non-kin (Bilde et al. 2002). In eusocial insects, cuticular hydrocarbons have been identified to convey specific information about the colony identity or the degree of relatedness (Lahav et al. 1999; Dani et al. 2005; d'Ettorre and Moore 2008). Hence, it seems reasonable to screen other arthropods for similar mechanisms. Grinsted et al. (2011) finally found evidence for cuticular hydrocarbons also mediating kin recognition in the subsocial spider *S. lineatus*. The hydrocarbon profiles of juvenile pre-dispersal spiders vary considerably, thus potentially carrying information about the family identity that can be used for kin discrimination. Behavioural experiments further demonstrated that the spiders preferably choose to reside next to cuticular chemical extracts of siblings (Grinsted et al. 2011). Moreover, the composition of branched alkanes as a subset of identified hydrocarbons is not substantially influenced by environmental factors underpinning a genetic basis of the substance makeup to be used as cues. Direct fitness benefits of cooperating with kin (see. Schneider 1996; Schneider and Bilde 2008) may have favoured selection towards using these cuticular substances as a kin recognition tool.

Summary

This overview reveals that social recognition abilities exist in various social and non-social arachnids. It allows individuals to distinguish between congeners, conspecifics, nestmates, and related and unrelated individuals to either support or discriminate against them. Interestingly, kin recognition also occurs in species that do not form groups. However, it is always linked to social interactions, at least in juvenile associations. The adaptive significance of these social behaviours resides in functions like increased protection, foraging efficiency and brood care and true cooperation in foraging, predator defence and cooperative breeding. However, the role of kin recognition as a mediator for these behaviours remains understudied.

In contrast to the eusocial insects, where kin recognition mediates both within- and between-colony interactions, the adaptive value of kin recognition in arachnids appears to be more context-dependent. It varies among species with differing sociality levels and life stages. Yet, kin recognition is accepted to have fitness benefits and has been suggested to play a role in the transition from subsocial to social living by promoting close kin associations. Possessing the ability to recognise and discriminate kin is particularly valuable for species that frequently interact with non-kin as it occurs in many subsocial species. By contrast, interactions with non-kin are rare in social species and thus selection may not favour the maintenance of recognition abilities. Accordingly, kin recognition has not been demonstrated in permanently social species yet.

The adaptive significance of kin recognition may be hard to discern, but sometimes it might simply be behaviourally undetectable. For example, the advantage of cooperation among related spiders might reside in performance differences in communal feeding events on a molecular level. Either individual spiders could contribute more or less digestive enzymes depending on who they are feeding with, or the digestive fluids of non-kin could be less compatible than those of kin. Through immunological differences, the enzymes themselves may compete inside the carcass of the prey resulting in a reduced effectiveness of the extra oral digestion in non-kin feeding groups. Here, the adaptive significance of kin recognition and kin discrimination may be very subtle. It might only manifest in the form of preferential association with kin for feeding. Thus, apart from simply detecting kin discrimination in particular species, future studies may need to screen more closely for specific contexts in which this ability appears to be adaptive. This has been exemplarily done in studies on preferential cannibalism among juveniles, but may be extended to other scenarios that influence the performance of groups, like foraging, feeding, brood care, defence etc. Another open question that needs to be answered in future investigations is the importance of kin recognition abilities for the transition from subsociality to permanently social group living. For that, we need to identify and to focus on transitional species to unravel crucial kin-selected trait(s) that facilitate the formation of permanent colonies. One of the key issues will be a better understanding of the recognition mechanisms and a clear distinction between the use of genetically based recognition cues and familiarity. Uncovering the evolutionary importance of social recognition in arachnids turns out to be a puzzle, generalisations may not be possible, and only a stepwise approach can provide us with a more comprehensive knowledge of their sociality.

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