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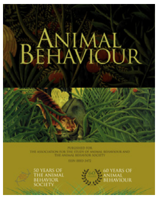

Smells familiar: group-joining decisions of predatory mites are mediated by olfactory cues of social familiarity☆

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Group-living animals frequently have to trade off the costs and benefits of leaving an established group and joining another group. Owing to their high fitness relevance, group-joining decisions are commonly nonrandom and may be based on traits of both individual members and the group such as life stage, body size, social status and group density or size, respectively. Many group-living animals are able to recognize and to associate preferentially with familiar individuals, i.e. those encountered before. Hence, after dispersing from established groups, animals commonly have to decide whether to join a new familiar or unfamiliar group. Using binary choice situations we assessed the effects of social familiarity on group-joining behaviour of the plant-inhabiting predatory mite *Phytoseiulus persimilis*. Group living in *P. persimilis* is brought about by the patchy distribution of its spider mite prey and mutual conspecific attraction. In the first experiment, gravid predator females given a choice between spider mite patches occupied by unfamiliar and familiar groups of females strongly preferred to join familiar groups and to deposit their eggs in these patches. Preference for socially familiar groups was robust across biases of spider mite prey densities between choice options. The second experiment revealed that the predatory mite females can smell social familiarity from a distance. Females subjected to odour choice situations in artificial cages were more strongly attracted to the odour of familiar than unfamiliar groups. We argue that *P. persimilis* females preferentially join socially familiar groups because a familiar social environment relaxes competition and optimizes foraging and reproduction.

Group living is a ubiquitous phenomenon in animals (Krause & Ruxton 2002; Earley & Dugatkin 2010). Widespread individual benefits of group living are, for example, enhanced vigilance, increased foraging success, reduced predation risk, or more mating opportunities and higher reproductive success. However, group living may also incur costs such as increased competition for shared resources and mates or increased disease transmission (Krause & Ruxton 2002; Earley & Dugatkin 2010). Individuals of group-living species are usually not permanently associated with a given group but are frequently faced with decisions to leave an established group and either join the next available one or search for another. Joining behaviour is defined as the nontransient association of a previously solitary individual with a given group (Prokopy & Roitberg 2001). Proximately, group-joining decisions may be based on diverse sensory modalities such as olfaction (Borden 1985; Campbell et al. 1993), vision (Langbein et al. 2004) or audition (Wijenberg et al. 2008). Ultimately, individuals should have evolved abilities to recognize and join those groups that provide the highest net fitness gains (Prokopy & Roitberg 2001; Krause & Ruxton 2002; Reddon et al. 2011). Accordingly, the trade-off between the costs and benefits of joining a given group poses a major challenge for group-living animals (Krause & Ruxton 2002; Earley & Dugatkin 2010).

The costs and benefits of joining a given group may depend on numerous interrelated traits at the individual and group level such as member life stage and body size (Ranta et al. 1992), competitive ability (Metcalfe & Thomson 1995), dominance hierarchy (Jordan et al. 2010), genetic relatedness (Ward & Hart 2003), social familiarity (Griffiths et al. 2004) or group size and density (Barber & Wright 2001). Accordingly, group-joining decisions may be based on various morphological, physiological, behavioural or ecological characteristics of a given group and its members, respectively.

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Owing to the high fitness relevance of social interactions, many group-living animals have evolved sophisticated abilities to assess the social status of group members such as the ability to discriminate unfamiliar from familiar individuals, that is, those with whom they interacted previously (Mateo 2004). Use of social familiarity for group-living decisions is known from both vertebrates and invertebrates and is especially well documented for fish (Brown & Colgan 1986; Miklosi et al. 1992; Brown & Smith 1994; Barber & Wright 2001; Jordan et al. 2010) but has also been observed in cattle (Hagen & Broom 2003), birds (Senar et al. 1990), mice (Szenczi et al. 2012), lizards (Moreira et al. 2008), cockroaches (Wijenberg et al. 2008), ants (Wilgenburg van 2007) and mites (Strodl & Schausberger 2012a, b, 2013; Zach et al. 2012). Social familiarity may allow better coping with the interrelated cognitive, behavioural and physiological challenges inherent to group living and thus optimize the group-living benefits. Potential advantages of preferential association with familiar individuals include foraging benefits (Dugatkin & Wilson 1992; Ward & Hart 2005; Strodl & Schausberger 2012a), improved antipredator behaviours (Chivers et al. 1995; Strodl & Schausberger 2012b), more effective transmission of information (Swaney et al. 2001), less intense competition for food (Metcalfe & Thomson 1995; Utne-Palm & Hart 2000), enhanced reproductive success (Strodl & Schausberger 2013) or facilitation of reciprocal behaviours (Croft et al. 2005; Zach et al. 2012).

In this study we assessed the influence of social familiarity on group-joining behaviour of the plant-inhabiting predatory mite *Phytoseiulus persimilis*. This species is a highly specialized predator of tetranychid mites such as the herbivorous two-spotted spider mite *Tetranychus urticae*. The spider mites are patchily distributed on their host plants and so are *P. persimilis* foraging, reproducing and developing in the spider mite patches (Sabelis 1985). In the prey patches the predators frequently encounter each other, providing opportunities to become familiarized with one another. Contact early in life, in the larval stage preceding the two nymphal stages, seems crucial for familiarization, with imprinting being an important learning mechanism used (Schausberger 2004, 2007; Strodl & Schausberger 2012a, b). The ability of *P. persimilis* to discriminate familiar from unfamiliar conspecifics, independent of genetic relatedness, has been observed in various contexts such as cannibalism (Schausberger 2007), within-group association, foraging and reproduction (Strodl & Schausberger 2012a, 2013), dispersal (Zach et al. 2012) and antipredator behaviour (Strodl & Schausberger 2012b). Close genetic relatedness is not a prerequisite for social familiarity but may add indirect fitness benefits, increasing inclusive fitness (Hamilton 1964a, b). The within- and between-plant distribution of *P. persimilis* is spatially and temporally dynamic (Nachman 1981, 2001), albeit not as pronounced as in fission–fusion societies, which are characterized by frequent merging, splitting and exchanging among groups such as shoaling fish (e.g. Croft et al. 2005). Prey patch residence and leaving decisions of *P. persimilis* are known to depend mainly on prey availability and competitor presence (e.g. Nachman 1981, 2001) but nothing is known about whether intraspecific behavioural traits such as social familiarity play a role in their group formation and joining dynamics. We conducted two experiments to assess whether social familiarity affects group-joining decisions of adult *P. persimilis* females. In the first experiment, gravid females were given a choice between spider mite prey patches occupied by unfamiliar and familiar females and their residence and oviposition preferences were assessed. Based on the results of the first experiment, in the second experiment we examined whether the predatory mite females respond to volatile chemosensory cues released by the familiar and unfamiliar groups.

METHODS

Origin and Rearing of Experimental Animals

Experimental animals were obtained from females drawn from a laboratory-reared population of *P. persimilis*, originally founded about 4 years ago with specimens field-collected in Valencia, Spain. The population was maintained on artificial rearing units each consisting of a plastic tile resting on a water-saturated foam cube (130 × 130 mm), placed in a plastic box (200 × 200 mm) half-filled with water and surrounded by water-saturated tissue paper. The predatory mites were fed with mixed life stages of *T. urticae*, reared on whole bean plants, *Phaseolus vulgaris*, by adding detached spider mite-infested leaves onto rearing units in 2–3-day intervals. Rearing units were stored at 25 ± 1 °C, 60 ± 5% relative humidity and 16:8 h light:dark.

Familiarization of P. persimilis

Arenas used to obtain predator eggs of similar age and subsequently to generate familiar individuals (familiarization arenas) consisted of single bean leaves placed adaxial surface down on a water-saturated foam cube (50 × 50 mm) in a small plastic box (100 × 100 mm) half-filled with water. Strips of tissue paper folded over the edges of the leaves prevented the mites escaping. Before adding the predators, we brushed mixed life stages of *T. urticae* onto the arenas. Each familiarization arena was furnished with six to eight gravid *P. persimilis* females, randomly drawn from the rearing units, and allowed to lay eggs for 24 h. After 24 h, the predator females were removed and their offspring reared to adulthood. Gravid females to be used in the experiment were randomly chosen from this arena and marked with a tiny watercolour dot on their dorsal shield for identification during the experiment. Familiar females, that is, those reared on the same familiarization arena, were marked with the same colour, but colours differed between familiarization arenas.

Experiment 1: Group-joining Decisions

Binary choice experiments were conducted to assess the influence of social familiarity on group-joining decisions of gravid *P. persimilis* females. Each experimental arena consisted of a pair of similarly sized leaflets, taken from trifoliate bean leaves, connected by a wax bridge. The leaflets, with the adaxial surface down and their bases facing each other, were placed about 40 mm apart on moist tissue paper covering a water-saturated foam cube (160 × 80 mm and 80 mm high), placed in a plastic box (200 × 100 mm and 100 mm high) half-filled with water. Each leaflet had an accessible area of 40 × 40 mm created by folding strips of moist tissue paper over the edges of each leaflet. The wax bridge (about 40 × 10 mm) connecting the two leaflets was created by dripping hot wax from a nonfragrant candle on the tissue paper (Vanas et al. 2006).

To provide sufficient prey eggs for the predators on the choice leaflets, 1 day before the predators were released we placed, on each pair of leaflets, 7–12 gravid *T. urticae* females, depending on the number of prey eggs needed for the experiment. After 24 h the *T. urticae* females were removed, the number of eggs laid was counted, and the required number of prey eggs was left on the leaflets according to the design of the experiment. If the number of spider mite eggs was above or below the required amount, eggs were removed or added using a fine camel hair brush. To assess the influence of prey density on the joining decisions of *P. persimilis*, we tested seven ratios of prey egg densities between the two leaflets, harbouring the familiar and unfamiliar females, respectively: