Animal Behaviour 127 (2017) 15–21

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Early social isolation impairs development, mate choice and grouping behaviour of predatory mites

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ARTICLE INFO

Article history:
Received 25 November 2016
Initial acceptance 24 January 2017
Final acceptance 10 February 2017

MS. number: 16-01035

Keywords:
group living
mite
sociability
social deprivation
social enrichment
stress

The social environment early in life is a key determinant of developmental, physiological and behavioural trajectories across vertebrate and invertebrate animals. One crucial variable is the presence/absence of conspecifics. For animals usually reared in groups, social isolation after birth or hatching can be a highly stressful circumstance, with potentially long-lasting consequences. Here, we assessed the effects of social deprivation (isolation) early in life, that is, absence of conspecifics, versus social enrichment, that is, presence of conspecifics, on developmental time, body size at maturity, mating behaviour and group-living in the plant-inhabiting predatory mite *Phytoseiulus persimilis*. Socially deprived protonymphs developed more slowly and were less socially competent in grouping behaviour than socially enriched protonymphs. Compromised social competence in grouping behaviour was evident in decreased activity, fewer mutual encounters and larger interindividual distances, all of which may entail severe fitness costs. In female choice/male competition, socially deprived males mated earlier than socially enriched males; in male choice/female competition, socially deprived females were more likely to mate than socially enriched females. In neither mate choice situation did mating duration or body size at maturity differ between socially deprived and enriched mating opponents. Social isolation-induced shifts in mating behaviour may be interpreted as increased attractiveness or competitiveness or, more likely, as hastiness and reduced ability to assess mate quality. Overall, many of the social isolation-induced behavioural changes in *P. persimilis* are analogous to those observed in other animals such as cockroaches, fruit flies, fishes or rodents. We argue that, due to their profound and persistent effects, early social deprivation or enrichment may be important determinants in shaping animal personalities.

The social environment experienced early in life has profound influences on developmental, physiological and behavioural trajectories (Monaghan, 2008; West, King, & White, 2003). A crucial variable is whether individuals can socially interact or not, and this is especially true for animals living in groups (Krause & Ruxton, 2002). Animals normally reared together, or living in groups, are adapted to experiencing and interacting with conspecific individuals after birth or hatching. For such animals, social isolation (i.e. deprivation of social contact) is a highly stressful circumstance, with potentially severe and persistent adverse consequences (Cacioppo & Hawkley, 2009; Fuller, 1967).

The effects of social isolation (deprivation) on interrelated physiological, life history and behavioural traits have been extensively studied in vertebrates including humans (e.g. Blanchard, McKittrick, & Blanchard, 2001; Cacioppo & Hawkley, 2009; Gluck & Harlow, 1971), also because of their enormous importance to health (House, 2001; Scotti, Carlton, Demas, & Grippo, 2015). The occurrence of early social environment effects is widespread across animal taxa, but their expression varies with taxon-specific biology and ecology. Commonly affected traits are somatic growth and development, longevity, cognitive development, hormonal balance and social behaviour. For example, cichlids reared in isolation grow more slowly, shoal less, have impaired learning abilities, and are more aggressive and less cooperative in antipredator behaviours than cichlids reared in groups (Brandão, Braithwaite, & Goncalves-de-Freitas, 2015; Hesse, Anaya-Rojas, Frommen, & Thünken, 2015). In zebrafish, persistent social isolation decreases brain serotonin levels, which is a widespread effect of social isolation across vertebrates, and anxiety-related

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http://dx.doi.org/10.1016/j.anbehav.2017.02.024

behaviours (Shams, Chatterjee, & Gerlai, 2015). The opposite occurs in chickens, in which social isolation increases anxiety (Suarez & Gallup, 1983). In mammals, social isolation commonly enhances defensiveness in subordinate individuals yet increases aggression in dominant ones (Blanchard et al., 2001). European rabbits reared in isolation suffer from reduced immune functions compared to those reared in groups (Rödel & Starkloff, 2014). Social isolation impairs white matter development and leads to abnormal connectomes in the brain cortex of adolescent rodents (Buwalda, Geerdink, Vidal, & Koolhaas, 2011; Liu et al., 2016). In nonhuman primates, social isolation early in life may impair sociability, decrease the ability to cope with stress, increase aggressiveness and/or lead to deficiencies in sexual and parental behaviours (for review, see Olsson & Westlund, 2007).

Analogous effects to those observed in vertebrates may occur in invertebrates. However, in comparison to vertebrates, social isolation in invertebrates is less extensively studied and less well understood, which particularly applies to behavioural effects. Most reports on social isolation (deprivation) in invertebrates deal with the effects on physiology and life history traits such as development or survival. For example, socially isolated ants have shorter life spans than those living in groups (Boulay, Quagebeur, Godzinska, & Lenoir, 1999; Koto, Mersch, Hollis, & Keller, 2015). Similarly, social isolation shortens longevity of *Drosophila* (Ruan & Wu, 2008). Mushroom bodies, which are important structures in insect brains for processing chemosensory inputs, of honeybees isolated early in life grow more slowly than those of bees reared in groups (Maleszka, Barron, Helliwell, & Maleszka, 2009). Socially deprived cockroaches develop more slowly, produce their oothecae later, are less exploratory, forage less and are less able to assess the quality of potential mates than those reared in groups (Lihoreau & Rivault, 2008; Lihoreau, Brepson, & Rivault, 2009; Woodhead & Paulson, 1983). Female cactus bugs reared in groups have a greater tendency to forage communally than those reared in isolation (Miller, Fletcher, Anderson, & Nguyen, 2012). Socially deprived male crickets are more aggressive towards females than socially experienced males (Kuriwada, 2016).

Here, we investigated the effects of complete social isolation early in life on development, body size at maturity, grouping behaviour and mate choice of the group-living plant-inhabiting predatory mite *Phytoseiulus persimilis*. *Phytoseiulus persimilis* is specialized to forage on spider mites of the family Tetranychidae. Group-living in *P. persimilis* is brought about by the patchy distribution of its prey and mutual attraction (Muleta & Schausberger, 2013; Sabelis, 1985; Strodl & Schausberger, 2012a, 2012b; Zhang & Sanderson, 1992). Gravid predatory mite females deposit their eggs inside the webbed patches/colonies of the spider mites, and the developing predator offspring, from larva to protonymph to deutonymph to adult, grow up together in their natal sites, provided that sufficient prey are available within the patch. The larvae are highly sensitive to environmental cues but do not need to feed to moult to the next stage, the protonymph, which is the first obligatory feeding stage (Strodl & Schausberger, 2012a, 2013). At 25 °C, total juvenile development from egg to adult takes about 7 days (Sabelis, 1985). Depending on the number and relatedness of the founder predator females, groups may consist of only kin or mixed kin and nonkin (Strodl & Schausberger, 2012a, 2013). If prey are scarce, offspring might find themselves in patches where they grow up alone, without having contact with conspecific individuals (Schausberger, 2004). Individuals reared in isolation are aggressive sibling cannibals, whereas those reared in a group avoid cannibalizing familiar individuals (Schausberger, 2004, 2007). Apart from cannibalism, the effects of early social isolation on interrelated life history and behavioural traits of *P. persimilis* are untested.

We hypothesized that social isolation early in life negatively affects early life history traits such as juvenile development and growth of *P. persimilis*, and makes them less sociable in grouping behaviour and less choosy in mate choice. We pursued these hypotheses in three separate experiments, in which we compared the behaviour of predatory mites having been isolated either in the larval and early protonymphal stage or throughout development and those reared in a group.

METHODS

Predatory Mite Origin and Rearing

Phytoseiulus persimilis used in experiments were derived from a population originally collected in Greece. In the laboratory, the predators were maintained in piles of detached bean leaves infested by two-spotted spider mites, *Tetranychus urticae*, placed on acrylic tiles (15 × 15 × 0.5 cm). Three times per week, spider mite-infested bean leaves were added onto the tiles, which rested on water-soaked foam cubes (15 × 15 × 5 cm) inside plastic trays (20 × 20 × 6 cm) half-filled with tap water. Strips of moist tissue paper were wrapped around the edges of the tile to prevent the predators and their prey from leaving the arena. *Tetranychus urticae* was reared on whole common bean plants, *Phaseolus vulgaris*. To obtain *P. persimilis* eggs for experiments, about 20–40 gravid females, recognizable by their expanded bodies, were randomly withdrawn from the stock population and placed on a detached leaf arena, harbouring spider mites as prey, for oviposition. Detached leaf arenas consisted of a trifoliate leaf placed upside down on a water-soaked foam cube (5 × 5 × 5 cm) inside a plastic box (10 × 10 × 6 cm), with wet tissue wrapped around the edges of the leaf. No ethical approval or specific permit was needed for rearing and experimental use of *P. persimilis* and *T. urticae*, which are neither protected nor endangered species.

Development (Experiment 1)

Predator eggs, <20 h old, were collected from oviposition arenas, with half of them singly placed into acrylic cages (subsequently dubbed 'isolated'), each supplied with 8 spider mite eggs, and the other half placed in groups of three into acrylic cages (subsequently dubbed 'grouped'), each supplied with 24 spider mite eggs. Each acrylic cage consisted of a circular cavity (diameter = 15 mm) laser-cut into an acrylic plate, closed at the bottom by gauze and on the upper side by a removable microscope slide (Schausberger, 1997). The cages were monitored twice per day in 8 and 16 h intervals for determining the developmental state of the predators. As soon as the predatory mites had reached the protonymphal stage, each individual ($N = 37$ for grouped and $N = 36$ for isolated) was removed from its cage and singly placed into a new cage, equipped with 12 spider mite eggs as prey, until reaching adulthood. When the mites had reached adulthood, their sex was determined. Each acrylic cage was meticulously cleansed with 75% ethanol, using cotton buds, before the experiment and was used only once in the experiment. Acrylic cages were kept at 25 ± 1 °C, 60 ± 5% relative humidity (RH) and a 16:8 h light:dark cycle.

Mating Behaviour and Body Size (Experiment 2)

Predator eggs, <48 h old, were collected from the oviposition arenas, and half of them singly placed on detached leaf arenas, each harbouring two ovipositing spider mite females, to generate isolated predators, and the other half placed in groups of three on arenas, each harbouring four spider mite females, to generate grouped predators. Eggs produced by the spider mite females