



Increased investment in the defence of high-value offspring by a superorganism

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Parental investment theory predicts that parents should adjust their investment in offspring defence according to offspring value (i.e. the probability they will contribute to the next generation). Although previous research has shown this offspring value prediction is generally supported in unitary organisms, the 'superorganisms' formed by advanced colonial organisms have rarely been tested, and never by direct manipulation of offspring value. As an important complement to correlational studies, such a test would help better illuminate the applicability of the parental investment theory to that higher level of biological organization, as well as provide insight into the depth of the superorganism analogy. Here I use colonies of the fire ant, *Solenopsis invicta*, in a manipulative experiment to test whether superorganisms behave as predicted by the parental investment theory and invest more in defence (deliver larger venom doses) when protecting higher-value offspring. In addition, to test a proposed mechanism for observed increases, I conducted an experiment to investigate whether *S. invicta* alarm pheromone modulates venom dose. I found that colonies delivered larger venom doses when defending nests containing higher-value (sexual) offspring than when defending worker-destined brood, but I found no venom dose increase as a result of additional alarm pheromone. The conformity of *S. invicta* colonies to the offspring value prediction of the parental investment theory supports the theory's applicability to their higher (super-organismal) level of animal organization. It furthermore underscores that the superorganism concept is deeper than simple anatomical/organizational analogy, but extends also to colony-level behaviour.

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Parental investment is any investment made by a parent that increases the offspring's chance of survival at the cost of the parent's ability to invest in other offspring (Trivers, 1972). This includes efforts to guard offspring, and parental investment theory predicts that parents should adjust their investment in offspring defence according to offspring value (Andersson, Wiklund, & Rundgren, 1980; Montgomerie & Weatherhead, 1988; Redondo, 1989). Offspring value can vary according to the number, age, size and/or quality of offspring (Carlisle, 1985; Winkler, 1987), and these factors can all be viewed as proxies for offspring reproductive value, i.e. the probability that they will contribute to the next generation (Patterson, Petrino, & James, 1980). Studies of parental investment generally focus on nest defence, and many correlative and experimental (although predominantly correlative) studies of parental defence have been conducted on birds (by far the most studied), fish, mammals and insects (birds: Greig-Smith, 1980;

Montgomerie & Weatherhead, 1988; Pavel & Bures, 2001; Redondo & Carranza, 1989; Rytönen, 2002; Rytönen, Orell, Koivula, & Soppela, 1995; Svagelj, Trivellini, & Quintana, 2012; fish: Carlisle, 1985; Colgan & Brown, 1988; Lavery & Colgan, 1991; Lavery & Keenleyside, 1990; Thünken, Meuthen, Bakker, & Kullmann, 2010; mammals: Jonsson, Agrell, Koskela, & Mappes, 2002; Maestripierei & Alleva, 2010; insects: Goubault, Scott, & Hardy, 2007; Judd, 1998; London & Jeanne, 2003; Seal, 2002). Although previous research has shown the offspring value prediction is generally supported in unitary organisms, colonies of advanced eusocial organisms, referred to as 'superorganisms' (Hölldobler & Wilson, 2009), have rarely been tested (although one was investigated by London & Jeanne, 2003).

Superorganisms are societies, typically advanced eusocial insect societies, whose organization can be viewed as analogous to the physiological organization of unitary organisms, with the reproductive queens (and the stored sperm of their mating partners) as gonads, and the sterile workers as somatic cells and tissues, etc. (Hölldobler & Wilson, 2009). This analogy applies to the colonies of many economically and ecologically important social insects, e.g. honey bees (*Apis*), leafcutter ants (*Atta*), driver ants (*Dorylus*), army

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ants (*Eciton*), weaver ants (*Oecophylla*), Argentine ants (*Linepithema*) and fire ants (*Solenopsis*) (Hölldobler & Wilson, 2009). As with unitary organisms, the offspring of superorganisms can be described as precocial or altricial, but superorganisms produce both types. The precocial offspring are the daughter colonies that result from the mating of female and male sexual castes (eggs and sperm in the superorganism analogy) and the subsequent founding of new colonies (or, as in some species, those daughters that result from colony fission). The altricial offspring are a colony's worker brood (immature stages) and sexuals (both brood and adult stages), which require the care and protection of the parent colony as they mature within their natal nest.

These two types of altricial offspring, at maturity, represent different values to the parent colony in terms of fitness; the sexuals convey fitness directly through the foundation of daughter colonies, while the workers, which themselves do not reproduce, do so indirectly through the performance of work for the colony. However, despite this clear difference in reproductive value, superorganisms may not behave in defence of these offspring as predicted by parental investment theory. Unlike unitary organisms, their altricial offspring (worker brood and sexual brood and adults) are intermixed within the 'soma' of the parent (the adult workers of the colony), so any threat to these offspring, regardless of their value to the parent, is a *de facto* threat to the parent as well. Thus, in superorganisms, selection for optimized offspring defence may have been superseded by selection for optimized self-defence, which would be expected to result in defensive behaviour that varies in relation to other factors, e.g. threat intensity, rather than in relation to secondary concerns such as offspring value.

Colonies of the fire ant, *Solenopsis invicta*, are superorganisms (Tschinkel & Wilson, 2014) that correlative data suggests may behave as predicted by the parental investment theory. In a seasonal study of nest defence in *S. invicta*, Haight and Tschinkel (2003) found that venom dose (i.e. the amount of venom workers delivered per sting) was higher in the spring than in the rest of the year. This venom dose increase in springtime, driven by the major workers (headwidths ≥ 0.90 mm), coincided with the annual pulse of sexual caste production by colonies (Tschinkel, 2006) and was interpreted as an increased colony investment in the defence of these valuable offspring (Haight & Tschinkel, 2003). However, this interpretation is based on correlation only, as the effect of the presence of sexuals on nest defence was not explicitly tested. While many previous studies have presented solely correlative evidence in support of the parental investment theory (e.g. Andersson et al., 1980; Barash, 1975; Biermann & Robertson, 1981; Blancher & Roberston, 1982; Greig-Smith, 1980; Lavery & Colgan, 1991; London & Jeanne, 2003; Pavel & Bures, 2001), manipulative experimentation is important if factors explaining observed correlations are to be resolved (Coleman, Gross, & Sargent, 1985). For example, in the wasp *Polybia occidentalis*, because investment in offspring production and in the complex activity of nest construction (Jeanne, 1986) are correlated, it is unclear to what extent a correlation between colony defensiveness and investment in brood may be due to offspring value or nest value (London & Jeanne, 2003).

Here I conducted a manipulative experiment to test whether the superorganisms formed by *S. invicta* behave as predicted by the offspring value prediction of the parental investment theory. I applied the 'pseudomutant' technique of Wilson (1980) and split individual *S. invicta* colonies into equally sized subcolonies with differing offspring value compositions and assayed whether they invested more in defence (delivered larger venom doses) when protecting higher-value offspring. This work represents the first test of the parental investment theory in a superorganism using a direct manipulation of offspring value. The paired experimental design furthermore holds constant potentially problematic factors

such as colony size, offspring number, nest construction investment and time. Such a test, an important complement to previous correlational studies, will help better illuminate the applicability of the parental investment theory to the superorganismal level of biological organization, as well as provide insight into the depth of the superorganism analogy.

In addition, to test a proposed mechanism for observed increases in venom dose, I conducted a similar experiment to investigate whether *S. invicta* venom dose increases in response to increased alarm pheromone. As alarm pheromone released at the nest during the initiation of mating flights is thought to promote the protection of sexuals through the induction of alarm behaviours and increased aggression/pugnacity in workers (Alonso & Vander Meer, 1997; Obin & Vander Meer, 1994), it is possible that alarm pheromone could also serve to mediate worker venom dose (Haight, 2006). High abundance could indicate threatened or damaged sexuals, as they contain around three times as much alarm pheromone as workers (Vander Meer, Preston, & Choi, 2010), or it could be indicative of a large number of alarmed or damaged workers. Both scenarios should merit a robust and decisive response from defending workers, which venom dose increases would provide through dose-dependent pain delivery and tissue damage (Read, Lind, & Oda, 1978).

METHODS

Effect of the Presence of Sexual Offspring on Nest Defence

I conducted this experiment in Tallahassee, FL (Leon County), U.S.A. during 12–24 April 2009. I collected ants from 10 different sexually producing monogyne *S. invicta* colonies by shoveling nest soil into 5-gallon (18.9-litre) plastic buckets with Fluon-coated insides to prevent escapes (Fluon TE-3859, DuPont, Wilmington, DE, U.S.A.). I transported them to the laboratory of Dr Walter Tschinkel at Florida State University where this experiment was conducted. I separated each colony's ants from their nest soil by spreading the ant–soil mixture as thinly as possible in well-lit, rectangular (56 cm long \times 71 cm wide \times 8 cm deep) Fluon-coated photo trays provided with dark, moist, plaster-floored petri dish nests in the corners. As the soil dried workers readily collected the colony's offspring (i.e. larvae, pupae and adult female and male sexual forms (alates)) and moved them into the inviting petri dish nests. I provided the ants with freeze-killed beetle larvae (*Zophobas* sp.) and cotton-stopped tubes of water and 20% sugar water at each petri dish nest. Periodic respreading of the soil aided drying and worker access to buried brood (larvae and pupae), which sped up the separation and consolidation process. In the four cases where I had coincidentally collected the queen, I removed her and set her aside with a small group of workers to tend her. At the conclusion of the experiment I returned the ants to their territories in the field.

Once separated from their nest soil, I placed the ants of each colony into a stacked series of three brass U.S. standard testing sieves with a solid bottom pan (W.S. Tyler, Inc., Mentor, OH, U.S.A.) in the following top-to-bottom sieve order: size 12 (1.70 mm openings), size 16 (1.18 mm openings) and size 18 (1.00 mm openings). I lit the tops of the sieve stacks with incandescent lights to encourage the ants to move through the screens as deeply as their respective sizes would allow, and I had coated the inner sides of the sieves and bottom pans with Fluon to ensure one-way movement down the stacks. This process was further encouraged through gentle tapping and shaking of the sieve stacks. The relatively large adult sexuals and late-stage sexual-destined brood (sexual larvae and pupae) were stopped by sieve sizes 12 and 16, while the adult workers and worker-destined brood (worker larvae and pupae) were stopped by sieve sizes 16 and 18, or passed

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