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Division of labour and risk taking in the dinosaur ant, *Dinoponera quadriceps* (Hymenoptera: Formicidae)

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Abstract

The success of social insects can be largely attributed to division of labour. In contrast to most social insects, many species with simple societies contain workers which are capable of sexual reproduction. Headed by one or a few reproductive individuals, subordinate workers form a dominance hierarchy, queuing to attain the reproductive role. In these species task allocation may be influenced by individual choice based on future reproductive prospects. Individuals with a better chance of inheriting the colony may be less likely to take risks and high-ranking workers that spend a greater amount of time in proximity to the brood may be able to increase the ability to police egg-laying by cheating subordinates. We investigated division of labour and risk taking in relation to dominance rank in the queenless ponerine ant, *Dinoponera quadriceps*, a species with relatively simple societies. Using behavioural observations, we show that high-ranking workers spend more time performing egg care, less time foraging and are less likely to defend the nest against attack. High-rankers also spent a greater amount of time guarding and inspecting eggs, behaviours which are likely to improve detection of egg laying by cheating subordinates. We also show that high-ranking workers spend a greater amount of time idle, which may help increase lifespan by reducing energy expenditure. Our results suggest that both risk-taking and egg-care behaviours are related to future reproductive prospects in *D. quadriceps*. This highlights a mechanism by which effective division of labour could have been achieved during the early stages of eusocial evolution.

Key words: Eusociality, *Dinoponera quadriceps*, social insect, dominance hierarchy, Ponerinae, polyethism.

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Introduction

Social insects represent one of the pinnacles of social evolution, and the evolution of eusociality is considered to be one of the major transitions in evolution (Maynard Smith & Szathmary 1995). Understanding how such highly co-operative societies evolved has been a key area of interest for evolutionary biologists since Darwin, who highlighted the apparent paradox of worker behaviour (Darwin 1859). One of the primary characteristics of eusocial societies is division of labour (Robinson 1992, Beshers & Fewell 2001), a stable variation within a colony in the tasks that individuals perform (Beshers & Fewell 2001). Division of labour is believed to have been a key factor in the success of social insects, increasing efficiency and maximising resource use (Wilson 1974, Wilson 1985, Page & Mitchell 1998). All social insect colonies show reproductive division of labour, where a relatively small number of individuals (queens) are responsible for reproduction, while the other colony members (workers) rear the young, forage and maintain the nest (Robinson 1992). In some species, the worker caste is further divided into individuals who specialise in certain tasks for at least part of their adult life (Wilson 1974, Robinson 1992, Wilson 2000). The majority of social insect species lack morphologically differentiated castes (Wilson 1974) and in these societies labour is often divided according to age, via temporal polyethism (Wilson 1974, Tofts 1991, Beshers & Fewell 2001). Most commonly, temporal polyethism involves younger workers performing tasks within the nest, and older workers leaving the nest to forage (Beshers & Fewell 2001). This results in individuals with a shorter life expectancy performing the more dangerous outdoor tasks (Kay & Rissing 2005, Moron & al. 2008).

In contrast to species with large, complex societies, species with small, relatively simple societies can sometimes contain workers who are physically capable of sexual reproduction, a state which is most likely ancestral in wasps and bees but which is secondarily derived in a number of ant species (Peeters 1991, Field & al. 2000). Reproduction is still dominated by one or a few individuals, however, and younger subordinate workers queue to take over the reproductive role (PEETERS 1991, SHREEVES & FIELD 2002, FIELD & CANT 2009).

Queuing for reproduction results in differences in the future reproductive prospects of different individuals in the colony (CANT & FIELD 2001, FIELD & CANT 2009). In these societies individual workers may select tasks based on the costs and benefits associated with them (CANT & FIELD 2001). Since high-ranking workers have a greater chance of future reproduction (PARDI 1948, MONNIN & PEETERS 1998, 1999) we might expect them to be less likely to engage in foraging and nest defence (CANT & FIELD 2001, FIELD & CANT 2009), tasks that are likely to have a high mortality rate (VISSCHER & DUKAS 1997, FIELD & CANT 2009). High-ranking individuals may also increase their chances of future reproduction by spending a greater amount of time idle, or by increasing body condition, for example by increasing time spent grooming (FIELD & CANT 2009). However, to our knowledge these hypotheses have not yet been thoroughly tested in a species in which worker reproduction is secondarily derived.

Although subordinate workers in species with simple societies may be physically capable of reproduction, there is in fact little opportunity for them to gain direct reproductive fitness because in some species (e.g., ants), males show no interest in mating with subordinates (PEETERS 1991). However, unmated workers are capable of laying male eggs, enabling them to gain direct reproductive fitness (RATNIEKS & VISSCHER 1989, MONNIN & RATNIEKS 2001). Widespread subordinate reproduction is likely to reduce colony productivity and in many species worker reproduction is deterred by policing (RATNIEKS 1988, RATNIEKS & VISSCHER 1989, LIEBIG & al. 1999, D'ETTORRE & al. 2004). However, some individuals still attempt to cheat and lay male eggs, leading to conflict within the colony. By spending more time performing egg care, high-rankers could remain in close proximity to the egg pile, where most conflict is likely to occur.

Within the eusocial Hymenoptera, reproductive totipotency and the absence of a morphologically distinct queen caste occurs in four main groups; within ants in the subfamily Ponerinae (PEETERS 1991), within bees in the subfamily Halictinae (sweat bees; DANFORTH 2002), and within wasps in the subfamilies Stenogastrinae (hover wasps) and Polistinae (paper wasps; HINES & al. 2007). Despite marked similarities in their social structure, primitively eusocial wasps, bees and ants differ in their evolutionary histories. The stenogastrine and polistine wasps, and halictine bees evolved independently from solitary ancestors (DANFORTH 2002, HINES & al. 2007). By contrast, queenless ponerine ants evolved from a highly eusocial ancestor with a morphologically distinct queen caste (PEETERS & CREWE 1984). If workers in queenless ponerine ants are capable of modifying their behaviour according to their future reproductive prospects, the mechanisms underlying this must have evolved along with or shortly after the loss of the sterile worker caste. Although rank has previously been found to affect risk-taking behaviour in two species of primitively eusocial wasp (O'DONNELL 1998, CANT & FIELD 2001, CRONIN & FIELD 2007), very little work has been done to investigate this phenomenon in species with secondarily derived worker reproductive totipotency.

The dinosaur ant, *Dinoponera quadriceps*, has small, simple, queenless societies, in which workers form a short, linear hierarchy behind the alpha (PEETERS & CREWE 1984, MONNIN & PEETERS 1999). When the alpha dies she is replaced by a high-ranked subordinate, most commonly the beta, and high-ranking workers themselves are frequently replaced by newly emerged workers, resulting in age-based hierarchy in which low-ranking workers are the oldest colony members (MONNIN & PEETERS 1999). Observations suggest that foraging and nest maintenance may tend to be carried out by lower ranked individuals and brood care by higher ranked individuals (MONNIN & PEETERS 1999), in keeping with hierarchical position affecting division of labour, but the data in support of this is still quite limited. Here we carry out a detailed examination of the relationship between dominance rank and behaviour in *D. quadriceps*. Using observations of 24 behaviours and experimental stimulation of nest defence we test the hypothesis that individuals exhibit different behaviours in relation to their current and future reproductive prospects. The effects of age and rank are confounded in this species, therefore we do not attempt to identify the mechanism but merely whether behaviour is related to reproductive potential. Specifically, we predict that (1) high-ranking workers show lower energy expenditure and avoid dangerous tasks such as foraging and nest defence, thereby increasing their chances of future reproduction, and (2) high-rankers spend a greater amount of time performing egg care, maximizing their ability to prevent and detect cheating. We predict that the reproductive female (alpha) and the highest ranking subordinate (beta) should engage more in egg guarding and egg antennation, as a means of preventing and detecting cheating amongst other high-rankers.

Materials and methods

Study species: *Dinoponera quadriceps* is found in Northeast Brazil, where it lives in colonies of between 40 and 100 workers (MONNIN & PEETERS 1998). The species constructs chambered nests, usually found at the base of trees, which extend up to one meter below ground (PAIVA & BRANDAO 1995). It is both predator and scavenger, feeding on a mixture of other insects and fruit (C.L. Asher, unpubl.). Fecundity in reproductives is relatively low and winged reproductives are only produced for the male sex, therefore new colonies are formed by fission of a small group (PEETERS 1991, BOURKE 1999, MONNIN & PEETERS 2008).

Collection and housing: Colonies of *Dinoponera quadriceps* were collected from Altantic forest in Sergipe (11° 01' 23" S, 37° 12' 9" W), Brazil in 2009 and 2010, and housed at 26 - 29°C, 70 - 90% relative humidity and a 12:12 light:dark cycle. Colonies were housed in plastic containers (38 cm × 58 cm × 18 cm) containing a plastic nest chamber (33 cm × 19 cm × 11 cm), divided into six compartments by a cardboard divider. Colonies were fed *Tenebrio* mealworms and banana three times a week, corned beef once a month, and provided with water ad libitum. To allow individual identification, all ants were tagged with a small unique number tag (E.H. Thorne Ltd). For each colony, a weekly census was performed to record the approximate number of eggs, larvae and pupae. Births and deaths were also monitored in order to maintain a record of the size of the colony.

Tab. 1: Description of all behaviours recorded during dominance observations, division of labour observations and nest defence experiment.

Behaviour	**Description**
Aggressive (dominance) Interactions	
Block	Actor stretches antennae on either side of the head of the recipient, which stands crouched. (Highest ranked dominance behaviour, characteristic of alpha – beta interactions).
Gaster Rub	Actor bites one antenna of the recipient and rubs it against her gaster (abdomen), which is curled forward.
Gaster Curl	Actor bites one antenna of the recipient, often pulling at it. The target often crouches, with her antennae folded against her head or stretched backward.
Antennal Box	Actor rapidly and repeatedly hits the head of the recipient with her antennae.
Immobilisation	One to six actors bite the recipients legs, antennae or mandibles and prevent her from moving, sometimes for up to several hours.
Leg Bite	A single actor bites the leg of a recipient worker, for one or two seconds. (Lowest ranked dominance behaviour).
Risky Tasks	
Forage	Actor moves around foraging area.
Nest Defence	Actor attacks foreign object, or leaves nest box in response to foreign object.
Brood Care	
Egg Antennate	Actor touches eggs with tips of antennae, sometimes moving egg with them.
Egg Carry	Actor carries a single or a pile of eggs.
Egg Guard	Actor stands in close proximity to the egg pile, with antennae squarely around eggs.
Larva Antennate	Actor touches larva with tips of antennae.
Larva Carry	Actor carries larva.
Larva Clean	Actor wraps mandibles around larva and licks surface of the larva.
Larva Feed	Actor places or arranges small food items on belly of larva to allow it to feed.
Larva Guard	Actor stands in close proximity to the larva, with antennae squarely around it.
Pupation Help	Actor assists larva to pupate by biting or wrapping silk around the larva as it is produced.
Pupa Antennate	Actor touches pupa with tips of antennae.
Pupa Carry	Actor carries pupa.
Pupa Guard	Actor stands in close proximity to the pupa, with antennae squarely around it.
Other Colony Tasks	
Waste Removal	Actor carries remains of prey items, dead nest mates or other pieces of waste out of the nest and places them on the waste pile in the foraging area.
Self Groom (inside / outside nest)	Actor cleans self using legs or mandibles. Location recorded.
Allogroom	Actor cleans recipient's body using mandibles.
Nest Maintenance	Actor bites or moves parts of the nest (tissue paper or cardboard divider).
Carry Food	Actor carries a prey item into or around nest.
Process Food	Actor bites prey item into smaller pieces, without consuming them.
Idle (inside / outside nest)	Actor is completely still. Location recorded.

Determining dominance rank: The dominance hierarchy in *Dinoponera quadriceps* is maintained by frequent ritualised aggressive interactions between high ranking workers (MONNIN & PEETERS 1999). These "dominance interactions" have been categorised into six types: blocking, gaster rubbing, gaster curling, antennal boxing, immobilisation and leg biting (MONNIN & PEETERS 1999) (Tab. 1). Blocking, where the actor stretches her antennae around the head of the recipient, is characteristic of interactions between the alpha and the beta (MONNIN & PEETERS 1999). These six interactions can be reliably used to determine dominance rank, which is correlated with ovarian activity (PEETERS & al. 1999). The aggressive interactions have been ranked, according to severity, by MONNIN & PEETERS (1999). Individuals who perform the greatest number of higher ranked interactions have a higher dominance rank.

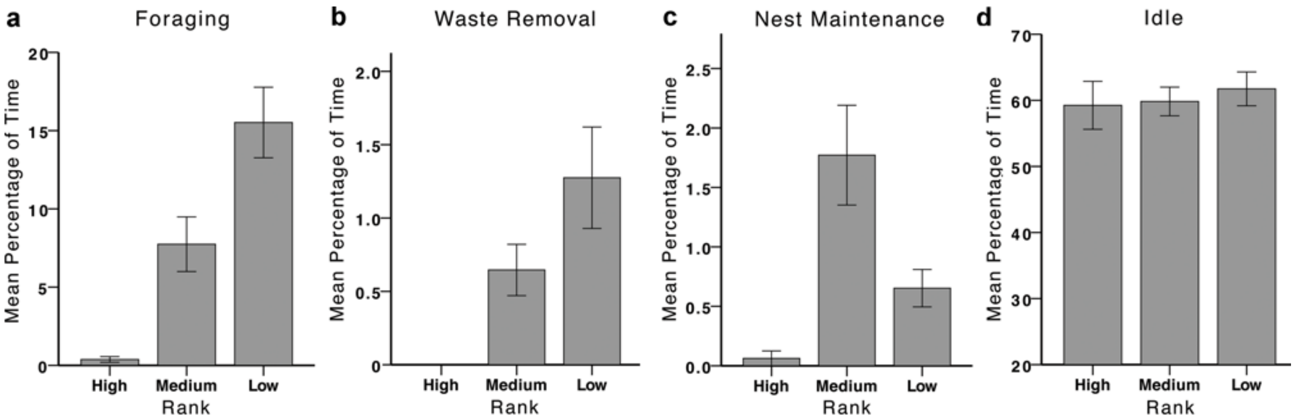

Fig. 1: Mean ± 1 standard error percentage of time spent performing a) foraging, b) waste removal, c) nest maintenance and d) idle for 142 *Dinoponera quadriceps* ants of high-, medium- or low-rank.

The identity of the alpha and high-ranking subordinates in six colonies (N = 142) was assessed using behavioural observations. Colonies were observed for 30-minute periods, during which the nature of any aggressive interactions was recorded. For each aggressive interaction observed, the type of interaction and the identity of the actor and recipient were recorded. Repeat occurrences of the same interaction between the same pair of individuals during one observation session were not recorded. Colonies were observed for a total of 18 hours 45 minutes (mean per colony 3:07 ± 0:54). Dominance hierarchies were then constructed for each colony. It was only possible using this method to assign precise linear ranks to high-ranking individuals, because of the rarity of aggressive interactions in medium- and low-rank classes. The remaining colony members were assigned to coarse-scale hierarchical categories; medium- and low-rank. Individuals were assigned to these categories based upon both the frequency and intensity of aggressive interactions observed (MONNIN & PEETERS 1999). High-ranking individuals are frequently involved in high intensity interactions (e.g., "blocking" and "gaster rubbing"), whilst medium-ranked workers are only rarely involved in aggression and usually of a low intensity (e.g., "immobilisation" and "antennal boxing"). Low-ranked workers are involved in aggressive interactions only extremely infrequently; when aggression does occur low-ranked workers are the recipients rather than the actors, and interactions are of low intensity.

Division of labour: The non-aggressive behaviours of all colony members (N = 142, mean colony size = 23.7 ± 4.6) were recorded during 100 spot-samples between 6th July and 7th September 2010. In total, 24 different behaviours were recorded (Tab. 1). Additionally, in order to control for the overrepresentation of low- and medium-ranking workers in *Dinoponera quadriceps* colonies, focal observations were performed with nine individuals (three of each rank) from three colonies, for six ten-minute periods each. In these observations, it was possible to differentiate idle individuals from individuals moving around the nest but with no clear task (henceforth termed as "walking").

Nest defence: To investigate nest defence behaviour, a two-phase nest defence experiment was performed. During the first phase, colonies were disturbed by repeatedly performing sharp taps in the foraging area with a pair of forceps. Individuals attacking the forceps during this phase were removed in sequence until there was no further response to tapping for 60 seconds. The second phase then began, during which the forceps were inserted into the nest entrance and removed again, repeatedly. Individuals attacking the tweezers or exiting the nest to defend were collected in sequence until no further response was generated for 60 seconds, at which point the trial ended. This was repeated for ten trials with each of six colonies.

Statistical analysis: Statistical analysis of the division of labour data was performed using a generalised linear mixed effects model approach in SPSS version 18. For each individual, the percentage of time spent engaging in each different activity was calculated. Each behaviour was tested against rank, with colony included as a random effect, using a poisson error distribution. The division of labour focal observation data was analysed using a repeated measures generalised linear mixed effects model with colony included as a random effect. For each ten-minute observation, percentage of time spent performing each behaviour was calculated and each behaviour was analysed against rank. The nest defence experiment was analysed using a proportional hazards regression survival analysis and a pairwise Kaplan-Meier survival analysis using the Breslow statistic, both performed in SPSS with defence as the event of interest.

Results

Dominance ranks: The dominance rank of a total of 142 individuals across six colonies was determined (mean colony size = 23.6 ± 4.6). Each colony contained a single alpha, with subordinate workers being composed, on average, of 7% ± 0.7 high-rankers, 37% ± 4 medium-rankers and 51% ± 4 low-rankers.

Risk taking: We predicted that high-ranking workers should spend less time foraging, removing waste and maintaining the nest, and be less likely to defend against attack. We found a significant effect of rank on proportion of time spent foraging ($F_{2,566} = 60.5$, $p < 0.001$). Low-rankers spent the most time foraging (15.5% ± 2.3), followed by medium-rankers (7.7% ± 1.8), with high-rankers foraging less than 1% (0.4% ± 0.2) of the time (Fig. 1a). There was no significant effect of rank on time spent removing waste from the nest ($F_{2,566} = 1.94$, $p = 0.148$, Fig. 1b). Nest maintenance was also significantly affected by rank ($F_{2,566} = 8.96$, $p < 0.001$), with medium-rankers engaging in this behaviour most often (Fig. 1c). There was a significant effect of rank

Tab. 2: Mean percentage of time spent performing different tasks for individuals of different rank. n = 142 individuals (six colonies).

Behaviour	**Mean**			
	All	**High-Rank**	**Medium-Rank**	**Low-Rank**
Aggression	< 1%	2.9% ± 0.9	0.4% ± 0.1	0.08% ± 0.04
Allogrooming	< 1%	0.6% ± 0.2	0.5% ± 0.1	0.2% ± 0.06
Carrying Food	1.3%	0.7% ± 0.5	1.2% ± 0.2	1.5% ± 0.2
Drinking	< 1%	0.2% ± 0.1	0.7% ± 0.1	1.2% ± 0.2
Eating	1.8%	2.3% ± 0.6	2.1% ± 0.2	1.5% ± 0.2
Egg Care	4.6%	14.1% ± 2.4	5.0% ± 0.9	2.4% ± 0.6
Foraging	11.2%	0.4% ± 0.2	7.7% ± 1.8	15.5% ± 2.3
Idle	60.8%	59.3% ± 3.6	59.8% ± 2.2	61.7% ± 2.6
Larva Care	2.6%	3.5% ± 0.9	4.0% ± 0.7	1.5% ± 0.3
Nest Maintenance	1%	0.06% ± 0.06	1.7% ± 0.4	0.7% ± 0.2
Pupa Care	1.9%	1.1% ± 0.4	2.8% ± 0.5	1.5% ± 0.3
Processing Food	1.4%	0.9% ± 0.3	1.6% ± 0.2	1.3% ± 0.2
Self Grooming	8.5%	6.9% ± 0.7	9.0% ± 0.6	8.5% ± 0.5
Waste Removal	< 1%	0%	0.7% ± 0.2	1.3% ± 0.3

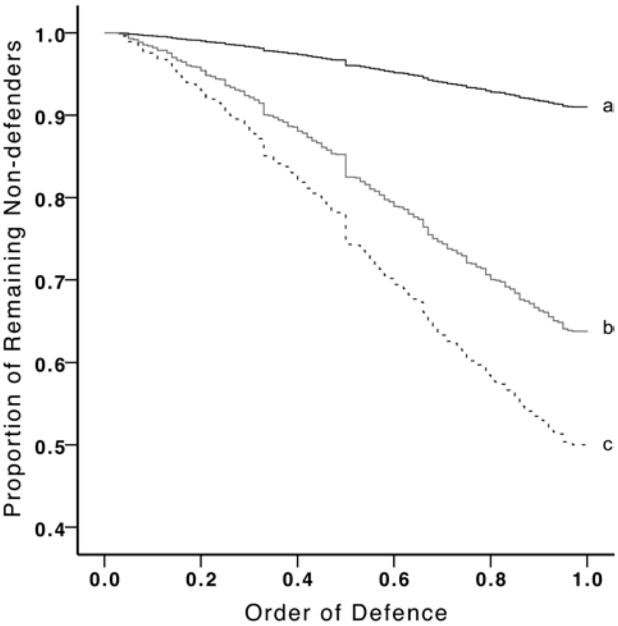

Fig. 2: Cox regression curve for order of nest defence behaviour, for individuals of different rank. Solid black line = high rank, solid grey line = medium rank, dotted line = low rank. Order ranges from zero for individuals who defended the nest first, to one for individuals who never defended. Letters indicate groups which were significantly different in Kaplan-Meier analysis.

on nest defence behaviour (Cox regression, $p < 0.001$). Low-rankers were the most likely to defend the nest, followed by medium-rankers, with high-rankers the least likely to defend (Fig. 2). Defence behaviour was also significantly affected by an individuals' location at the beginning of the defence trial (Cox regression, $p < 0.001$), however, the effect of rank was still highly significant when starting location was controlled for (LMER, $F_{2,566} = 34.686$, $p < 0.001$). The effect of rank was significant for all pairwise combinations (Kaplan-Meier, $p < 0.001$).

Activity levels: We hypothesised that high-ranking individuals would spend more time idle and self-grooming in order to maximise lifespan. All individuals spent the majority of their time idle (60.8% ± 1.8). The most common active behaviours were self-grooming, foraging and brood care (Tab. 2). There was a significant effect of rank on the proportion of time spent idle outside the nest ($F_{2,566} = 16.8$, $p < 0.001$) but the effect was not significant for time spent idle inside the nest ($F_{2,566} = 0.47$, $p = 0.629$). However, data from the focal observations showed a significant effect of rank on time spent idle inside the nest, ($F_{2,68} = 67.8$, $p < 0.001$). These conflicting results were due to the fact that during focal observations walking was differentiated from being completely idle, which was not possible during spot observations.

For grooming behaviour, there was a significant effect of rank on the proportion of time spent self-grooming inside ($F_{2,566} = 3.38$, $p = 0.038$), with medium-rankers spending the greatest time performing this behaviour. Time spent self-grooming outside the nest was also significantly correlated with rank ($F_{2,566} = 8.56$, $p < 0.001$), being primarily performed by low-ranking workers. This is consistent with a role of self-grooming in reducing pathogen load, since low-ranking foragers are likely to be exposed to the greatest number of pathogens. The effect of rank was also significant for time spent allogrooming others ($F_{2,566} = 4.75$, $p = 0.001$). High- and medium-rankers spent more time allogrooming other individuals than low-rankers did (0.6% ± 0.2 compared to 0.5% ± 0.1 and 0.2% ± 0.06). This is contrary to our expectation that low-rankers should perform the most allogrooming to improve the health of high-ranking colony members. Low-rankers may refrain

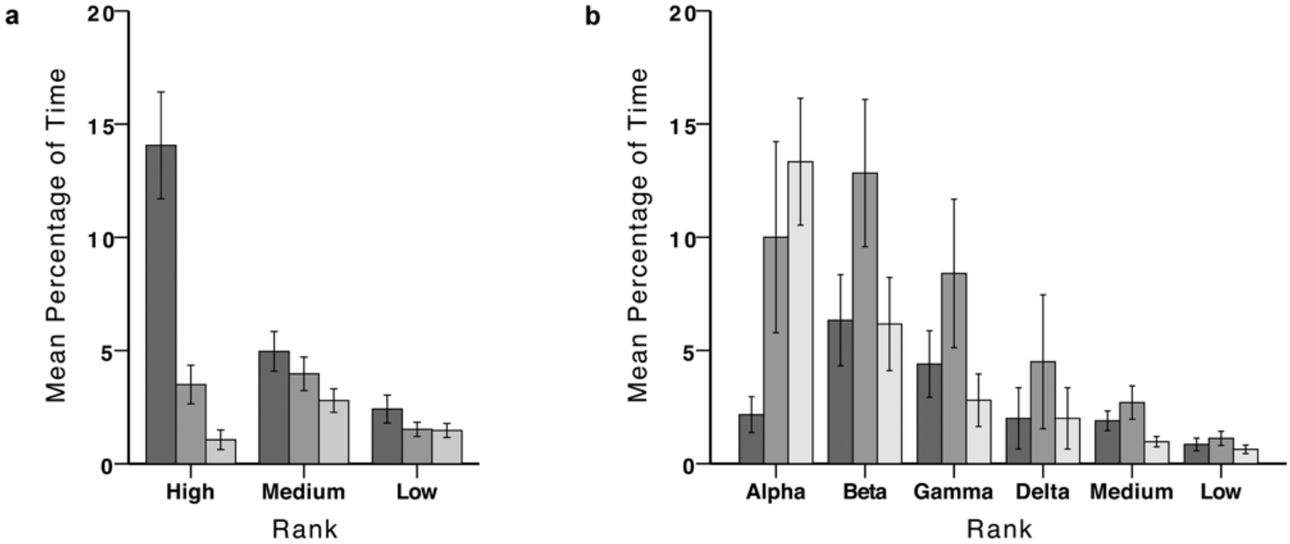

Fig. 3: Mean ± 1 standard error percentage of time spent performing brood care activities for individuals of different rank. a) Egg care (dark grey), larva care (medium grey) and pupa care (light grey) for high-, medium- and low-rank individuals. b) Egg antennation (dark grey), egg guarding (medium grey) and egg carrying (light grey) for each of the four top-ranking individuals, and medium- and low-rankers.

from grooming and in general minimise contact with other workers in order to minimise the opportunity for the transfer of potentially harmful pathogens which they may have obtained whilst foraging. High-rankers spent only a very small proportion of their time being aggressive towards other workers (2.9% ± 0.9) and aggressive behaviour was almost completely absent in medium- (0.4% ± 0.01) and low-rankers (0.08% ± 0.4). High-rankers spent significantly more time eating ($F_{2,566} = 3.47$, $p = 0.034$) and less time drinking ($F_{2,566} = 3.76$, $p = 0.026$). The effect of rank on all other behaviours investigated was non-significant. Results from focal observations were consistent with those from spot observations presented so far; the only exception being that time spent idle inside the nest was significantly affected by rank in the focal observations but not in the spot observations.

Brood care: Hypothesis two predicted that high-ranking individuals would perform more brood care, specifically egg care, enabling them to remain in close proximity to the site of potential cheating. Rank had a significant effect on all types of egg care behaviour, with high-rankers performing more egg care than other ranks (Fig. 3a). There was a significant effect of rank on proportion of time spent egg antennating ($F_{2,566} = 30.87$, $p < 0.001$), egg carrying ($F_{2,566} = 110.46$, $p < 0.001$) and egg guarding ($F_{2,566} = 112.69$, $p < 0.001$). Within high-rankers, there was a significant effect of rank on proportion of time spent guarding eggs ($F_{4,91} = 11.24$, $p = 0.001$) and egg carrying ($F_{4,91} = 5.17$, $p = 0.008$), with the alpha and beta performing more of each behaviour than other high-rankers. There was also a significant difference between high-rankers in the time spent egg antennating ($F_{4,91} = 4.44$, $p = 0.0014$). The beta performed significantly more antennation than the alpha ($t = -2.326$, df = 15, LSD $p = 0.034$, Figure 3b), whilst all other pairwise comparisons were non-significant. There was a significant effect of rank on proportion of time spent larva antennating ($F_{2,566} = 9.27$, $p < 0.001$), larva cleaning ($F_{2,566} = 5.10$, $p = 0.007$), larva guarding ($F_{2,566} = 11.50$, $p < 0.001$) and larva carrying ($F_{2,566} = 3.60$, $p = 0.03$). Medium-rankers performed the most antennating and cleaning, whilst high-rankers were responsible for the most larvae guarding behaviour. The effect of rank was not significant for larva feeding ($F_{2,566} = 1.50$, $p = 0.227$). There was no significant difference between larva care behaviour within high-rankers for any of the behaviours recorded. The effect of rank was not significant for pupa antennating ($F_{2,566} = 1.05$, $p = 0.353$), pupa guarding ($F_{2,566} = 1.22$, $p = 0.299$) or helping a larva to pupate ($F_{2,566} = 2.136$, $p = 0.122$). However, there was a marginally non-significant effect of rank for pupa carrying ($F_{2,566} = 2.94$, $p = 0.056$), with medium-rankers performing this task most often.

Discussion

Our results show a strong relationship between rank and behaviour in *Dinoponera quadriceps.* This is consistent with individual behaviour relating to future reproductive prospects, and suggests that the autonomy of queenless ponerine ant workers has increased since the divergence from their recent highly eusocial ancestor. Our results are consistent with previous studies of division of labour and risk taking in other species (FRANKS & SCOVELL 1983, MONNIN & PEETERS 1999), which have shown a tendency for subordinate colony members to take more risks.

While our data show that behaviour is related to reproductive potential in dinosaur ants, the results do not allow us to distinguish whether the relationship is driven by age or by age-independent effects of rank. Effects of age on behaviour are well known from across the social insects (WINSTON 1987, NAUG & GADAGKAR 1998, SEID & TRANIELLO 2006, HURD & al. 2007, JOHNSON 2008) and dominance rank is likely to be correlated with age in this species because newly emerged workers tend to enter near the top of the hierarchy (MONNIN & PEETERS 1999). Thus both age and rank are expected to be correlated with reproductive potential and direct fitness, and age may then be a useful criterion for an individual to estimate reproductive potential if the correlation is reasonably strong. However, the correlation between age and reproductive potential is unlikely to be perfect in species such as *Dinoponera quadriceps*, especially if many new workers emerge simultaneously, and age-independent mechanisms of assessing reproductive potential are therefore likely to be advantageous. Individual variation in fertility and the effects of this on behaviour are well known from honey bees (AMDAM & al. 2004, AMDAM & al. 2006) and has also been shown to affect how quickly *Platythyrea punctata* ponerine ants switch from in-nest work to foraging (WALTER 2012), so such age-independent effects are possible. Most probably a combination of mechanisms is used, with the simple criterion provided by age being complemented by more precise information provided by physiological factors such as fertility.

High-ranking individuals spent significantly less time foraging and were less likely to engage in nest defence, in keeping with the hypothesis that high-ranking individuals avoid performing tasks that are associated with high mortality risk. Foraging has previously been shown to be one of the most dangerous colony tasks (SCHMID-HEMPEL & SCHMID-HEMPEL 1984, VISSCHER & DUKAS 1997) and nest defence will also carry significant risks. Previous investigations into nest defence behaviour in cooperative vertebrates and primitively eusocial insects have produced extremely mixed results. In Damaraland mole rats it is the dominant individual who defends the nest against conspecific intruders (COONEY 2002), a pattern similar to hover wasps (CRONIN & FIELD 2006), paper wasps (FISHWILD & GAMBOA 1992) and halictine bees (BELL & al. 1974). In contrast to this, in naked mole rats, subordinates defend the nest (LACEY & SHERMAN 1991, O'RIAIN & JARVIS 1997), as we have also shown to be the case in *Dinoponera quadriceps*. These differences in colony defence strategy may be due to differing evolutionary histories. Nest defence by subordinates in queenless ponerine ants could be a characteristic left over from their highly eusocial ancestor, whereas colony defence by dominant individuals in species descended from a solitary ancestor may be a remnant of natural maternal defence of offspring. An alternative explanation may relate to differing colony sizes, as both naked mole rats and queenless ants have comparatively larger colony sizes. The opportunity for future reproduction in subordinates varies in relation to colony size (BOURKE 1999, MONNIN & al. 2003), and thus in species with very small colonies, subordinates may be unwilling to defend the nest.

Focal observations of individual behaviour revealed a strong relationship between rank and time spent idle. Several studies have found that workload negatively influences longevity (SCHMID-HEMPEL & WOLF 1988, TSUJI & al. 1996) and thus high-rankers should be expected to minimise energy expenditure (CANT & FIELD 2001), increasing their likelihood of surviving to obtain the reproductive role. We also predicted that high-rankers might spend more time performing self-grooming, a self-directed behaviour which is likely to improve longevity by reducing pathogen load (HUGHES & al. 2002, FERNÁNDEZ-MARÍN & al. 2006). In contrast to this, we found that medium-rankers performed the greatest amount of self-grooming inside the nest, and low-rankers performed the most outside the nest. However, this is consistent with self-grooming as a mechanism to reduce pathogen load, as medium- and low-ranking foragers are likely to be exposed to pathogens more frequently than non-foragers. Individuals are often observed self-grooming immediately after returning to the nest from a foraging trip, which further supports a key role for self-grooming in disease resistance. We found that high-ranking workers perform the most allogrooming, an unexpected result since allogrooming is expected to improve the health of the recipient. This may possibly indicate that allogrooming plays a social role in *Dinoponera quadriceps* (e.g., in maintaining hierarchies), similar to in many primates and other animals (REN & al. 1991, VERVAECKE & al. 2000, LAZARO-PEREA & al. 2004).

Brood care was primarily performed by high-ranking individuals, consistent with our hypothesis that this enables them to remain in close proximity to eggs, improving their ability to detect and prevent illicit laying by subordinate workers. Furthermore, egg care behaviours are mostly performed by high-rankers, a relationship that is not true for all larva and pupa care behaviours. Whilst all brood care behaviours are performed in the brood chamber, only the egg stage offers a significant opportunity for cheating. That high-rankers dominate this behaviour but not other brood care activities supports a role for egg care in preventing illicit egg laying. Previous investigations of egg-policing behaviour in this species have indicated that destruction of worker-laid eggs is performed primarily by the alpha, however, other high-rankers are also occasionally involved (MONNIN & PEETERS 1997). One surprising result is that the beta performs the greatest amount of egg antennation, as we might expect the alpha to have greatest incentive to inspect eggs in order to confirm that they were laid by her. However, it is possible that antennation also enables the beta to assess the fertility of the alpha, and thus judge whether it would be beneficial to attempt to overthrow her. It has previously been shown that ponerine ants are able to distinguish between alpha- and worker-laid eggs, which differ in their cuticular hydrocarbon profile (MONNIN & PEETERS 1997, TANNURE-NASCIMENTO & al. 2009) and that alpha fertility is also signalled through cuticular hydrocarbons (MONNIN & al. 1998, CUVILLIER-HOT & al. 2004). It is therefore plausible that by regularly antennating alpha-laid eggs, the beta may be able to assess her fertility. Attempts to overthrow the alpha will generally be met by high levels of aggression from low-ranking subordinates (MONNIN & al. 2002) except when alpha fertility is below 75% (MONNIN & RATNIEKS 2001). Since the beta rank changes regularly, the ability to detect an opportunity to overthrow the alpha represents a major fitness advantage for the beta (CUVILLIER-HOT 2004).

To our knowledge, this study is the first to demonstrate a relationship between future reproductive prospects and nest defence and other risk-taking behaviours in a species in which simple society is secondarily derived. The apparent flexibility in task choice exhibited by *Dinoponera quadriceps* is likely to have evolved relatively recently, since their divergence from their highly eusocial ancestor. Understanding the organisation of division of labour in simple eusocial societies can greatly inform explanations of the evolution of sociality itself.

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