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A Novel Method of Assessing Dominance Hierarchies Shows Nuance, Linearity and Stability in the Dinosaur Ant *Dinoponera quadriceps*

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Abstract

Many social species with relatively simple societies have dominance hierarchies of individuals, with dominant individuals achieving fitness and subordinate individuals either queuing to obtain fitness or achieving only indirect fitness by helping relatives. Assessing the dominance hierarchy in a social group is generally based upon observing dyadic interactions as and when they occur spontaneously within the whole-group setting. However, this method can be very time-consuming because many dyads interact only very rarely, necessitating either extremely long observation periods or many dyadic relationships being unresolved. Here, we report an alternative method using the queenless dinosaur ant *Dinoponera quadriceps*, which lives in colonies containing tens of individuals. We removed all individuals from their nest and observed the dominance behaviours expressed in isolated dyadic interactions for every pairwise combination of individuals. Individuals showed a classic dominance behaviour in this setting, and the rapid nature of the assay allowed us to observe every dyadic relationship on a weekly basis over 4 weeks. The dominance hierarchies based on these isolated dyadic interactions correlated well with those produced by the conventional method of colony observations. They showed the hierarchies to be highly linear and stable, and also revealed that dominance relationships may extend further down the hierarchy than previously thought. Although highly manipulative, the isolated dyadic interaction method works well and will likely make more feasible the study of other social species in which pairs of individuals can be isolated together.

Introduction

Many species live in groups, and the evolution and maintenance of social structures within those groups depend on the kinds of interactions among individuals. Patterns of social interactions influence different aspects of social living (Dey et al. 2013), including reproductive allocation (Herrera & Macdonald 1993; Monnin et al. 2002), the evolution of cooperation (Ohtsuki et al. 2006; Voelkl & Kasper 2009) and the transmission of disease or information (Wey et al. 2008; Godfrey et al. 2009). Many species readily form dominance hierarchies, both in nature and the laboratory, and importantly, once stable, these hierarchies can function to regulate conflicts over access to resources, reproduction and territories (Huntingford & Turner 1987; Aureli & de Waal 2000). Understanding such dominance relationships is therefore a key step in investigating the evolution of sociality.

Dominance hierarchies have been found in many social organisms including invertebrates and vertebrates (Huntingford & Turner 1987; Graham & Herberholz 2009; Hewitt et al. 2009; Chiarati et al. 2010). These hierarchies are social structures where there is a dominant relationship between all individuals in a group, and two individuals are defined as having a dominance relationship if one chases, threatens or bites its opponent, but its opponent typically offers no aggression and yields (Chase et al. 2002; Hewitt et al. 2009). Linear dominance hierarchies and the ranks of individuals typically remain stable for long periods of time under static conditions and when groups are small (Graham & Herberholz 2009; Chiarati et al. 2010). Interestingly, dominance hierarchies established via behavioural interactions in animal societies often dictate which individuals reproduce. Insect societies in particular, including ants where morphologically specialised reproductives are lacking (i.e. in approx. 100 species of ants where the queen caste has been lost secondarily; Monnin & Peeters 1999), offer an ideal opportunity for investigating such social structures because interactions among individuals can be readily observed repeatedly and under controlled conditions.

Dominance hierarchies in social insect colonies, as well as social groups of other animals, are typically determined by observation of dominance behaviours between individuals in the group. This has two disadvantages. First, it is extremely laborious, typically requiring very many hours of observation to collect data on replicated behavioural interactions for a good proportion of the group. This then restricts the feasibility of repeating the assessment, for example over time or after experimental manipulations. Second, there may often be many individuals in a group for which no dominance interactions are recorded within the observation period, or for which no interactions are recorded at all, which is a particular problem for those individuals that are relatively low ranked. In cases where individuals interact but do not express dominance, this may or may not be informative with regards to hierarchical position, but if individuals do not interact at all then it is uninformative. This results in conclusions about the social relationships having to be based on only a subset of the group. Although this may not be an issue for studies in which dominance only needs to be known for higher ranked individuals, it requires assumptions about hierarchy length and the irrelevance of dominance for individuals below the position for which data are obtained. These assumptions may not always be supported, particularly in species which have been little studied or in which lower ranked individuals may retain some potential for direct reproduction. It would therefore be useful to develop a method that allows the dominance relationships of individuals to be assessed more rapidly and in such a way that the relationships between every dyad can be determined. Here, we demonstrate such a method in the dinosaur ant *Dinoponera quadriceps*, based on isolated dyadic interactions (IDI). We compare the results of the IDI approach with that from conventional behavioural observations of whole colonies and use the more data-rich IDI method to assess the linearity and stability of the dominance hierarchy.

Methods

Dinoponera quadriceps is a queenless ponerine ant with relatively small societies (tens of individuals) in which the morphologically identical females form a near-linear dominance hierarchy (Monnin & Peeters 1999; Monnin et al. 2003). The alpha female is the functional equivalent of the queen, being the only individual to mate and reproduce sexually, with the remainder of the colony acting as workers to carry out all other tasks in the colony. Individuals generally eclose as the beta or another high rank, displacing the existing high-ranked individuals further down the hierarchy. Periodically, the beta will replace the alpha, mate and take over the reproductive role in the colony. High-ranked individuals (beta, gamma, delta, etc.) tend to avoid risky tasks and instead focus on caring for eggs and larvae (Monnin & Peeters 1999; Nascimento et al. 2012; Asher et al. 2013), which both maintains their reproductive potential and facilitates their ability to on occasion cheat to achieve direct fitness by laying unfertilised eggs that will develop into males if they are not policed (i.e. detected and removed) by their nestmates. The dominance hierarchy is regulated by direct behavioural interactions and indirectly by the alpha placing a pheromone on a challenger, which stimulates other members of the colony to immobilise the challenger (Monnin & Peeters 1998; Monnin et al. 2002).

Five colonies of *Dinoponera quadriceps* were used in the study (Dq092, Dq096, Dq097, Dq0910 and Dq0912). The colonies were collected in Sergipe, Brazil, in 2009 and, subsequently, maintained at 27 ± 2°C, 80 ± 10% RH, with a 12:12 light:dark cycle, on a diet of mealworms (*Tenebrio molitor*), banana and corned beef, with water provided *ad libitum*. Colonies were housed in plastic boxes

(33 × 19 × 11 cm) that were subdivided into six compartments with cardboard and kept within larger plastic boxes (38 × 58 × 18 cm) to provide a foraging area. All ants in the colonies were marked with individual numbered tags (E. H. Thorne Ltd.). Colonies Dq092, Dq096, Dq097, Dq0910 and Dq0912 contained respectively 9, 13, 10, 33 and 21 individuals at the start of the study ($\bar{x} \pm$ SE 17.2 ± 4.5).

To determine the dominance hierarchies via the conventional method, each colony was observed for 180 min over a 14-day period, with each observation bout taking place in early afternoon and lasting 90 min. This was shorter than in some other studies because the colonies here were also smaller, and the time period was sufficient to capture very similar conventional hierarchical information to that found in other studies (Monnin & Peeters 1999; Monnin et al. 2003; Asher et al. 2013). All dominance interactions between ants in a colony were recorded during these observation bouts. *D. quadriceps* ants show six dominance behaviours: blocking, gaster rubbing, gaster curling, antennal boxing, immobilisation and leg biting (Monnin & Peeters 1998). Blocking involves the dominant individual placing her antennae on either side of the head of the subordinate ant, gaster rubbing and gaster curling involve the dominant ant releasing pheromones with or without applying them directly to the subordinate ant, and antennal boxing involves the dominant ant rapidly and repeatedly tapping the head of the subordinate with her antennae. Blocking is exclusively carried out by the alpha, most commonly towards the beta and was therefore used to identify these individuals. Gaster rubbing and gaster curling were used to identify gamma and sometimes delta, while antennal boxing was used to determine the hierarchical position of lower ranked individuals.

We also determined the dominance hierarchies of the colonies using an isolated dyadic interaction method based on an approach used previously for bumblebees (Amsalem & Hefetz 2010). All ants were transferred from a colony into individual pots (10 cm diameter × 4 cm height) and left for 2 min to acclimatise. Pairs of ants were then placed into a new pot together and their dominance interactions observed. When manipulated carefully in this way, any alarm behaviours, such as gaping mandibles (Hughes & Goulson 2001; Hughes et al. 2001), were rare and extremely short-lived when they did occur. Only one dominance behaviour took place in this setting: dominant ants would stand tall and place their antennae on either side of the head of the subordinate ant, with the subordinate ants placing their body close to the floor with the antennae pulled back behind the head. This was essentially the same as the blocking behaviour observed during conventional observations of colonies, but in the novel assay was observed between all ranks of individuals, whereas in whole colonies it is only observed between alpha and normally beta. Generally, this dominance interaction occurred within 15 s of the ants being placed together, but it sometimes took up to 60 s to occur, particularly when both ants were low ranked, and in some low-ranked dyads, no dominance interactions were observed. Once all dyadic combinations had been tested, the ants were replaced in their nest where they appeared to behave normally thereafter. Testing all pairwise combinations of individuals in this way took from approx. 86 min for the smallest colony with nine individuals to 1094 min for the largest colony with 33 individuals ($\bar{x} \pm$ SE 380 ± 189 min). These isolated dyadic interaction assays were repeated every week for 4 wk.

Statistical Analysis

The outcomes of the isolated dyadic interactions (dominant, subordinate and no interaction) were organised into sociometric matrices and analysed using Matman 1.1 (Noldus Information Technology, Wagingen; de Vries et al. 1993). To compare the relationships produced by the conventional assessment of whole colonies with that produced by the IDI in the 4 wk, we converted the rankings into numerical values with 1, 2, 3, 4 and 5, equating to alpha, beta, high, medium and low for each colony. For IDI data with more complex hierarchies, we simplified it by scoring high/medium as 4 and medium/low as 5, in order that all hierarchies were on the same numerical scale. We then examined the relationships using Spearman's rank correlations. The linearity of the dominance hierarchies was determined using Landau's linearity index h' corrected for unknown and tied relationships (Landau 1951; de Vries 1995). This varies from 0 (complete absence of linearity) to 1 (complete linearity), with an $h' > 0.9$ being considered linear (Martin & Bateson 1993). The statistical significance of h' was calculated using a right-tailed probability value (p_r) from 10 000 randomisations (Kurvers et al. 2009). The dominance relationships of any three individuals can be either circular (A dominates B, B dominates C and C dominates A) or transitive (A dominates B and C, B dominates C), and Landau's linearity statistic tests for the transitivity of the dominance structure. The stability of the dominance hierarchies over time was tested using a Spearman's rank correlation, with hierarchies with ρ > 0.7 over time being considered stable (Oliveira & Almada 1996).

Results

The conventional assessment of whole colonies produced hierarchies of 2–5 high-rank individuals per colony (18 ± 4% of individuals per colony, x̄ ± SE) for which clear dominance relationships were determined, with remaining individuals being classified as either medium or low rank. Alpha was dominant to every other ant in her colony, beta was subordinate only to alpha, gamma was subordinate only to alpha and beta, and delta was subordinate only to alpha, beta and gamma. Medium-ranked individuals performed at least one instance of antennal boxing but no other dominance behaviours. Individuals that did not perform agonistic behaviours towards other individuals, either because they were only the recipients of dominance behaviours or because there were not involved in any dominance interactions at all, were categorised as low-ranked; low-ranked ants also spent much of their time outside of the nest chamber. While medium- and low-ranked individuals were presumed to be dominant or subordinate to members of other tiers, their relationships with other members of the same tier were uncertain. The hierarchies produced by the isolated dyadic interaction (IDI) method were more detailed, providing the dominance relationship and relative hierarchical position for every combination of individuals in the colony (between 36 relationships for nine individuals in Colony Dq092 and 528 relationships for 33 individuals in Colony Dq0910). Individuals broadly consisted of five dominance tiers: high, high/medium, medium, medium/low and low. As above, individuals in the high tier had unequivocal relationships with each other. Individuals in each of the other tiers, however, were established as being dominant or subordinate to members of the other tiers, but showed codominance with other individuals from the same tier.

The dominance hierarchies produced by the IDI assays correlated well with those produced by the conventional assessment of whole colonies, with the correlations being highly significant for all 4 wk in which IDI data were collected (Week 1: ρ = 0.564, N = 87, p < 0.001; Week 2: ρ = 0.526, N = 85, p < 0.001; Week 3: ρ = 0.52, N = 82, p < 0.001; Week 4: ρ = 0.476, N = 82, p < 0.001). The same individuals were identified as the alphas with both methods and in all weeks, and the same individuals were also identified as the beta, with the exception of Colony Dq0912 in Week 4 where the beta was ranked as gamma. The majority of high, medium and low-ranked individuals were also ranked the same by both methods and across weeks (Fig. 1; Fig. S1). Collecting

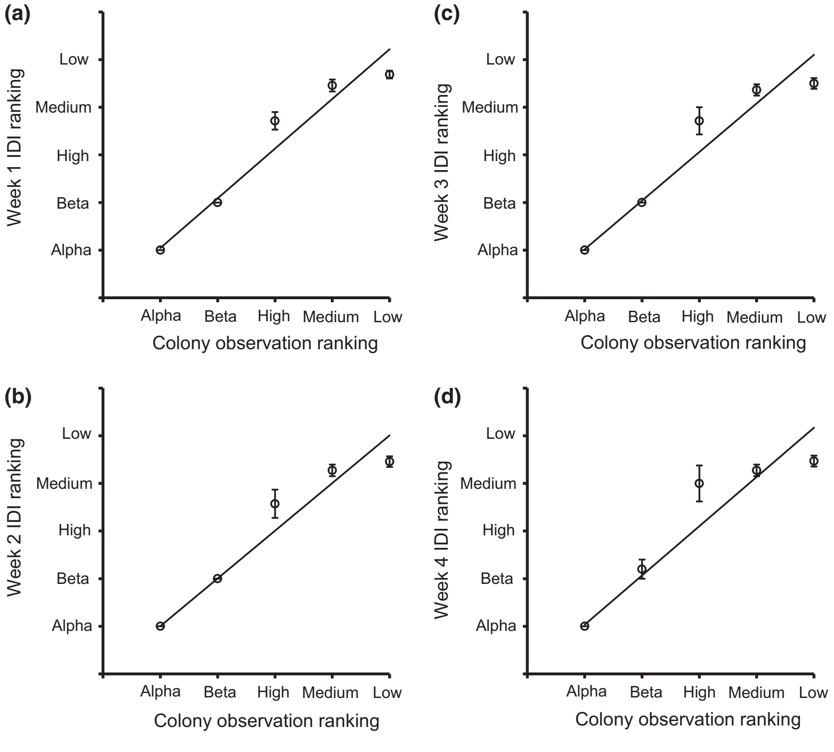

Fig. 1: Relationships between social rankings of dinosaur ants based on colony observations and the x̄ ± SE individual dyadic interaction (IDI) data for the (a) 1st week (b) 2nd week, (c) 3rd week and (d) 4th week. Lines of best fit are (a) $y = 1.04x$; (b) $y = 1.01x$; (c) $y = 1.02x$; and (d) $y = 1.03x$.

IDI data on multiple occasions and then averaging the ranks did not increase the strength of the correlation with the conventional assessment method (ρ = 0.539, N = 87, $p < 0.001$). Indeed, the strength of the relationship decreased slightly over the 4-week period which, to at least some extent, was due to the death of some individuals and to new individuals entering and disrupting the hierarchies. In addition to the case of the beta in Colony Dq0912 which the IDI data suggested was demoted to gamma in Week 4, there were also a high ranker in Colony Dq096 and another in Colony Dq0910 which appeared to be demoted to a low rank over the course of the 4-week period.

The dominance hierarchies produced by the IDI assays were strongly and significantly linear in all five colonies and in all 4 wk ($p < 0.01$ in all cases), with an overall mean h' of 0.95 (Fig. 2a; $p < 0.001$). Of the 15 week-to-week transitions across the five colonies, ten were stable based on a ρ > 0.7. The hierarchies in Colonies Dq092 and Dq096 were stable across all week-to-week transitions, those in Colonies Dq0910 and Dq0912 were unstable in one of the three week-to-week transitions (although in Colony Dq0910 this was only marginally so; ρ = 0.67), and the hierarchy in Colony Dq097 was relatively unstable across all three week-to-week transitions (Fig. 2b). Accordingly, there was overall a strong and highly significant correlation between the hierarchies produced by the IDI data in the first and last weeks of data collection (ρ = 0.599, N = 82, $p < 0.001$; Fig. 2c; Fig. S2).

Discussion

Using the dinosaur ant, *Dinoponera quadriceps*, as a model, we demonstrate an alternative method for determining dominance hierarchies. We show that observing isolated dyadic interactions allows the identification of dominance relationships among all individuals in a colony and did not disturb the social hierarchies in the colonies. Additionally, we find that the results obtained using this method are in strong agreement with results found using conventional methods of observing unmanipulated entire colonies, but provide greater resolution. In keeping with previous studies, the conventional method resolved the relationships for 2–5 individuals per colony into a linear hierarchy, with remaining individuals being categorised into broad tiers and there being many individuals for which no dominance interactions were observed at all (Monnin & Peeters 1999; Monnin et al. 2003; Asher et al. 2013). Using the IDI method, complete dominance relationships between all individuals were obtained (9–33 individuals per

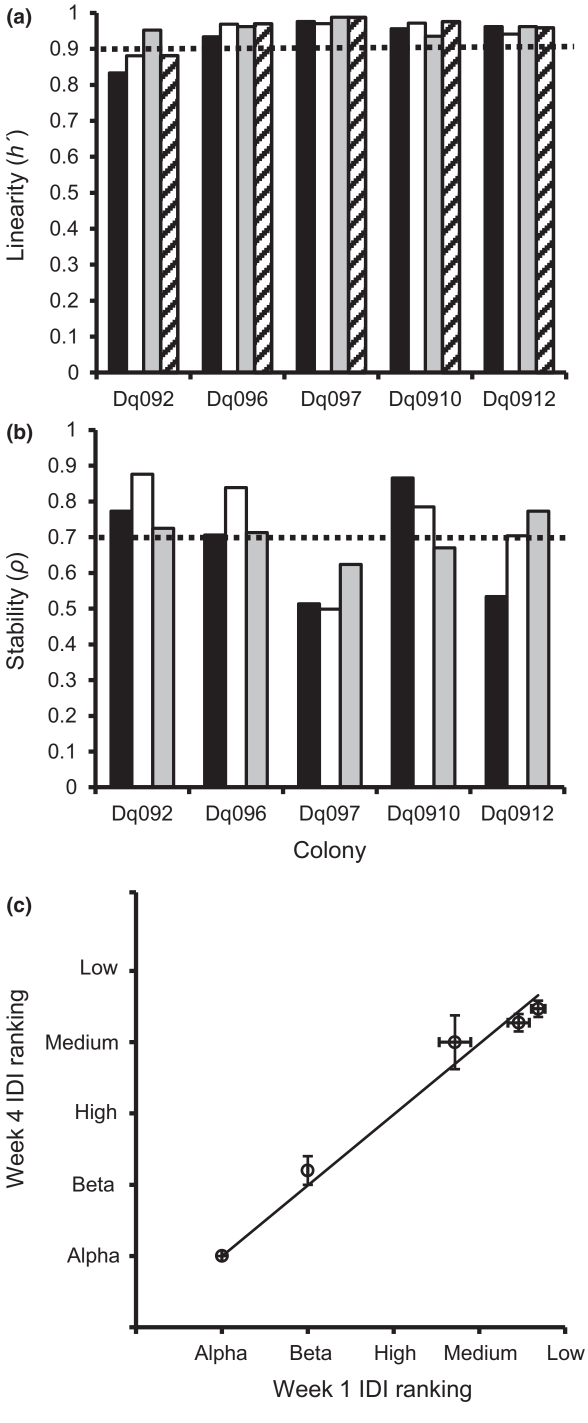

Fig. 2: The linearity (a) and stability (b) of dominance hierarchies in five *D. quadriceps* dinosaur ant colonies based upon Isolated Dyadic Interactions (IDI) data, and (c) the relationship between the $\bar{x} \pm$ SE hierarchical positions recorded in the 1st and 4th weeks of IDI. Linearity is Landau's h' index for 4 wk (weeks 1, 2, 3 and 4 being black, white, grey and hashed, respectively), and stability is Spearman's ρ for three week-to-week transitions (transitions for weeks 1–2, 2–3 and 3–4 being black, white and grey, respectively). The equation of the line of best fit in (c) is $y = 0.994x$.

colony; 36–528 dyadic relationships), revealing that hierarchies were highly linear and stable, and more complex than suggested using conventional methods. The IDI method did require a significant time investment to achieve this, taking between approx. 86 and 1094 min, depending on the size of the colony, compared with the 180 min of observation we carried out during the conventional method and longer periods in some other studies (Monnin & Peeters 1999; Monnin et al. 2003). This limits the application of the IDI approach for the study of social groups, although no more than for conventional observation. Whether the greater resolution provided warrants the IDI approach for the complete group, or whether an effective compromise is to utilise the IDI method with a targeted group of, for example, medium-rank individuals for which greater resolution is specifically needed, will of course depend on the precise research questions in a study.

Observations of isolated dyadic interactions in dinosaur ant colonies accurately predicted dominance hierarchies determined under natural colony conditions. Further, we find that the ant colonies appeared to behave normally once they were reassembled in their nest after each round of IDI assays. Therefore, although the IDI method employed here is highly manipulative, this method has the potential to be useful for investigating dominance relationships in social species, and furthering understanding of the causes and consequences of social living. As predicted when social group hierarchies take the form of a reproductive queue, and also shown in the whole-colony context, social conflict was highest and unequivocal in higher ranked individuals. Such individuals are more likely to gain a breeding position and therefore benefit more from changes in rank (Cant et al. 2006; Dey et al. 2013). Intuitively such high-ranking individuals are expected to invest more in dominant displays or behaviours (Cant et al. 2006), here observed as the tall standing ants in the IDI setting. In line with this possibility, aggression levels in several species of social insects, including dinosaur ants, have been shown to be influenced by rank rather than the other way around (Chandrashekara & Gadagkar 1992; Monnin & Peeters 1999; Cant et al. 2006). Similarly, in cooperatively breeding cichlid fish, certain pairs of individuals were found to experience greater social conflict relative to other dyads, and social conflict was highest towards the top of the hierarchy (Dey et al. 2013). Further, aggression rates increase with social rank in several other social vertebrates (Araba & Crowelldavis 1994; Muller & Wrangham 2004).

Specifically, the hierarchies identified here by the conventional assessment of whole colonies consisted of three dominance tiers: high, medium and low. High ranks consisted of 2–5 individuals, which were likely to be actual or hopeful reproductives that tend eggs and larvae, and avoid foraging or nest defence (Monnin & Peeters 1999; Nascimento et al. 2012; Asher et al. 2013). Relationships between individuals within the medium- and low-ranked tiers were uncertain, and indeed, the low-ranked individuals included many for which no dominance interactions were observed at all. The proportions of individuals in a colony identified as high, medium and low ranks here were comparable to those reported in other studies with this species, indicating that longer observation periods would have been unlikely to significantly improve the resolution (Monnin & Peeters 1999; Monnin et al. 2003; Asher et al. 2013). The IDI method provided a far more detailed assessment of hierarchy, with precise information on the relationship for every combination of individuals. This revealed a five-tier ranking, established the codominance of individuals within the lower ranked of these tiers and identified hierarchies as being highly linear, more so than conventional whole-colony observations had suggested before. Further, hierarchies defined using this method were found to be generally very stable. The only demotions observed over the course of the 4 wk assessment period were of single individuals in three colonies (Colonies Dq096, Dq0910 and Dq0912), which may have been challengers to the hierarchy that were unsuccessful and consequently demoted (Monnin & Peeters 1998; Monnin et al. 2002). Interestingly, hierarchical stability and linearity as found here, is predicted to be characteristic of animals living in smaller groups than typically found in *D. quadriceps* (<10 individuals), as larger group sizes can lead to irregularities in hierarchical order (Kaufmann 1993; Jameson et al. 1999). For example, cooperatively breeding carrion crows have been shown to have linear hierarchies that remain stable throughout the breeding season and across years (Chiarati et al. 2010). Similarly, in the green swordtail (*Xiphophorus hellerii*), individual rankings are robust even after experimental group fusions, or a change of social context (Earley & Dugatkin 2006).

Broadly, the results we obtained suggest that the IDI method may be useful for determining dominance relationships in social species and that *D. quadriceps* hierarchies are remarkably robust despite relatively large group sizes. Although the IDI method is highly manipulative, and the conventional method has the advantage of observing spontaneous expressions of dominance behaviours under more natural conditions, the dominance hierarchies produced by the two methods correlated well. We note that dominance across taxa can be context dependent, with an animal's status or ranking depending in part on the context that it is obtained in (Bernstein & Gordon 1980; Nelissen 1985; Cristol et al. 1990; Wiley 1990; Verbeek et al. 1999; Vervaecke et al. 1999; Chase et al. 2002). Such context dependency will of course need to be considered in future studies utilising the IDI method. However, the IDI method has the potential to aid understanding of dominance relationships for many social species.

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Literature Cited

Amsalem, E. & Hefetz, A. 2010: The appeasement effect of sterility signaling in dominance contests among *Bombus terrestris* workers. Behav. Ecol. Sociobiol. **64**, 1685—1694.

Araba, B. D. & Crowelldavis, S. L. 1994: Dominance relationships and aggression of foals (*Equus caballus*). Appl. Anim. Behav. Sci. **41**, 1—25.

Asher, C. L., Nascimento, F. S., Sumner, S. & Hughes, W. O. H. 2013: Division of labour and risk taking in the dinosaur ant, *Dinoponera quadriceps*. Myrmecol. News **18**, 121—129.

Aureli, F. & de Waal, F. B. M. 2000: Natural Conflict Resolution. Univ. of California Press, Berkeley, CA.

Bernstein, I. S. & Gordon, T. P. 1980: The social component of dominance relationships in rhesus monkeys (*Macaca mulatta*). Anim. Behav. **28**, 1033—1039.

Cant, M. A., Llop, J. B. & Field, J. 2006: Individual variation in social aggression and the probability of inheritance: theory and a field test. Am. Nat. **167**, 837—852.

Chandrashekara, K. & Gadagkar, R. 1992: Queen succession in the primatively eusocial tropical wasp *Ropalidia marginata* (Lep) (Hymenoptera: Vespidae). J. Insect Behav. **5**, 193—209.

Chase, I. D., Tovey, C., Spangler-Martin, D. & Manfredonia, M. 2002: Individual differences versus social dynamics in the formation of animal dominance hierarchies. Proc. Natl Acad. Sci. USA **99**, 5744—5749.

Chiarati, E., Canestrari, D., Vera, R., Marcos, J. M. & Baglione, V. 2010: Linear and stable dominance hierarchies in cooperative carrion crows. Ethology **116**, 346—356.

Cristol, D. A., Nolan, V. & Ketterson, E. D. 1990: Effect of prior residence on dominance status of dark-eyed junicos, *Junico hyemalis*. Anim. Behav. **40**, 580—586.

Dey, C. J., Reddon, A. R., O'Connor, C. M. & Balshine, S. 2013: Network structure is related to social conflict in a cooperatively breeding fish. Anim. Behav. **85**, 395—402.

Earley, R. L. & Dugatkin, L. A. 2006: Merging social hierarchies: effects on dominance rank in male green swordtail fish (*Xiphophorus helleri*). Behav Processes **73**, 290—298.

Godfrey, S., Bull, C., James, R. & Murray, K. 2009: Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. Behav. Ecol. Sociobiol. **63**, 1045—1056.

Graham, M. E. & Herberholz, J. 2009: Stability of dominance relationships in crayfish depends on social context. Anim. Behav. **77**, 195—199.

Herrera, E. A. & Macdonald, D. W. 1993: Aggression, dominance, and mating success among capybara males (*Hydrochaeris hydrochaeris*). Behav. Ecol. **4**, 114—119.

Hewitt, S. E., Macdonald, D. W. & Dugdale, H. L. 2009: Context-dependent linear dominance hierarchies in social groups of European badgers, *Meles meles*. Anim. Behav. **77**, 161—169.

Hughes, W. O. H. & Goulson, D. 2001: Polyethism and the importance of context in the alarm reaction of the grass-cutting ant, *Atta capiguara*. Behav. Ecol. Sociobiol. **49**, 503—508.

Hughes, W. O. H., Howse, P. E., Vilela, E. F. & Goulson, D. 2001: The response of grass-cutting ants to natural and synthetic versions of their alarm pheromone. Physiol. Entomol. **26**, 165—172.

Huntingford, F. A. & Turner, A. 1987: Animal Conflict. Chapman, London.

Jameson, K. A., Appleby, M. C. & Freeman, L. C. 1999: Finding an appropriate order for a hierarchy based on probabilistic dominance. Anim. Behav. **57**, 991—998.

Kaufmann, J. H. 1993: The Origins of Order. Oxford Univ. Press, Oxford.

Kurvers, R., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C. & Prins, H. H. T. 2009: Personality differences explain leadership in barnacle geese. Anim. Behav. **78**, 447—453.

Landau, H. G. 1951: On dominance relations and the structure of animal societies: I. Effects of inherent characteristics. Bull. Math. Biophys. **13**, 1—19.

Martin, P. & Bateson, P. 1993: Measuring Behaviour: an Introductory Guide. Cambridge Univ. Press, Cambridge.

Monnin, T. & Peeters, C. 1998: Monogyny and regulation of worker mating in the queenless ant *Dinoponera quadriceps*. Anim. Behav. **55**, 299—306.

Monnin, T. & Peeters, C. 1999: Dominance hierarchy and reproductive conflicts among subordinates in a monogynous queenless ant. Behav. Ecol. **10**, 323—332.

Monnin, T., Ratnieks, F. L. W., Jones, G. R. & Beard, R. 2002: Pretender punishment induced by chemical signalling in a queenless ant. Nature **419**, 61—65.

Monnin, T., Ratnieks, F. L. W. & Brandão, C. R. F. 2003: Reproductive conflict in animal societies: hierarchy length increases with colony size in queenless ponerine ants. Behav. Ecol. Sociobiol. **54**, 71—79.

Muller, M. N. & Wrangham, R. W. 2004: Dominance, aggression and testosterone in wild chimpanzees: a test of the ‘challenge hypothesis’. Anim. Behav. **67**, 113—123.

Nascimento, F. S., Souza, D., Tannure-Nascimento, I. C. & Dantas, J. O. 2012: Social facilitation and food partitioning in the queenless ant *Dinoponera quadriceps* (Hymenoptera: Formicidae). J. Nat. Hist. **46**, 1959—1967.

Nelissen, M. H. J. 1985: Structure of the dominance hierarchy and dominance determining group factors in *Melanochromis auratus* (Pisces, Cichlidae). Behaviour **94**, 85—107.

Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. A. 2006: A simple rule for the evolution of cooperation on graphs and social networks. Nature **441**, 502—505.

Oliveira, R. F. & Almada, V. C. 1996: On the (in)stability of dominance hierarchies in the cichlid fish *Oreochromis mossambicus*. Aggress. Behav. **22**, 37—45.

Verbeek, M. E. M., De Goede, P., Drent, P. J. & Wiepkema, P. R. 1999: Individual behavioural characteristics and dominance in aviary groups of great tits. Behaviour **136**, 23—48.

Vervaecke, H., De Vries, H. & Van Elsacker, L. 1999: An experimental evaluation of the consistency of competitive ability and agonistic dominance in different social contexts in captive bonobos. Behaviour **136**, 423—442.

Voelkl, B. & Kasper, C. 2009: Social structure of primate interaction networks facilitates the emergence of cooperation. Biol. Lett. **5**, 462—464.

de Vries, H. 1995: An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. **50**, 1375—1389.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993: Matman: a program for the analysis of sociometric matrices and behavioral transition matrices. Behaviour **125**, 157—175.

Wey, T., Blumstein, D. T., Shen, W. & Jordan, F. 2008: Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim. Behav. **75**, 333—344.

Wiley, R. H. 1990: Prior residence and coat-tail effects in dominance relationships of male dark-eyed junicos, *Junico hyemalis*. Anim. Behav. **40**, 587—596.

Supporting Information

Additional supporting information may be found in the online version of this article at the publisher’s web-Site:

Figure. S1: Relationships for each of five *Dinoponera quadriceps* dinosaur ant colonies between social rankings of dinosaur ants based on colony observations and the Individual Dyadic Interaction (IDI) data for the (a) 1st week (b) 2nd week, (c) 3rd week and (d) 4th week. Size of bubbles indicates the number of overlapping data points. Results of correlation analyses in each case are detailed within the graphs. Note that the individual colonies contained only 8–33 ants, and the correlation analyses for individual colonies consequently had limited statistical power.

Figure. S2: Relationships for each of five *Dinoponera quadriceps* dinosaur ant colonies between social rankings of dinosaur ants based on the Individual Dyadic Interaction (IDI) data for the 1st week and 4th week. Size of bubbles indicates the number of overlapping data points. Results of correlation analyses for each colony are detailed within the graphs. Note that the individual colonies contained only 8–33 ants, and the correlation analyses for individual colonies consequently had limited statistical power.