Division of labour within teams of New World and Old World army ants

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In army ants, prey items are often retrieved by cooperative teams of workers rather than by single porters. We used experiments and randomization tests to explore the division of labour within such teams in the New World army ant *Eciton burchelli*, and the Old World army ant *Dorylus wilverthi*. We evaluated these teams in the light of a recent proposal that teams should be defined in terms of the concurrent performance of different subtasks by their members. This is a broader and more useful definition of teams than a previous one in which teams were defined by a membership necessarily involving different castes. Within army ant teams there is a front runner who initiates prey retrieval and one or more followers. Hence, there are two qualitatively different subtasks that must be performed concurrently during such teamwork. Previous work has shown that these teams are superefficient: the combined weight of the prey retrieved by the team is greater than the sum of the maximum weights the team members could carry when working singly. Here we show, for both species of army ant, that such teams have a nonrandom composition of members. The front runner is typically unusually large and the second-largest ant in a team is typically unusually small. These analyses are based on worker dry weights rather than assigning workers to discrete caste categories. Our analysis also suggests that the behaviour of army ants is more sophisticated then previously suspected. Our data imply that if an unnecessarily large supplementary ant (follower) tries to help the front runner to move a large prey item, but finds that the remaining work is too slight to use her full efforts, she does not join the team. One or more smaller ants whose efforts become fully employed become involved instead. This suggests that army ants engaged in teamwork have both upper and lower workload thresholds.

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Recently, Anderson & Franks (in press) proposed a new definition of teamwork in animal societies, which can be applied to both invertebrates and vertebrates. They suggested that a team is defined in terms of the concurrent performance of different subtasks by their members. In other words, teams have a division of labour with, at least temporary, specialization among their members. For example, such teams occur during hunting in chimpanzees, *Pan troglodytes* (Dugatkin 1997), African wild dogs, *Lycaon pictus* (McFarland 1985), lions, *Panthera leo* (Stander 1992), and Galapagos, *Buteo galapagoensis*,

and Harris' hawks, *Parabuteo unicinctus* (Faaborg & Bednarz 1990).

Teams were first demonstrated by Franks (1986) in insect societies. He showed that not only are prey retrieval groups in the New World army ant *Eciton burchelli* superefficient, with a collective performance that is more than the sum of the isolated performances of its members, but they also have a nonrandom caste composition. Hölldobler & Wilson (1990) defined teams, based on the discoveries of Franks (1986), as 'members of different castes that come together for highly co-ordinated activity in the performance of a particular task'. This definition restricts the existence of teams to societies in which there are recognizable castes. The new definition of Anderson & Franks (in press) is consistent with the work of Franks (1986), but frees the concept of teams from the issue of caste composition. By recognizing that the central issue is the concurrent performance of different subtasks, which may or may not involve

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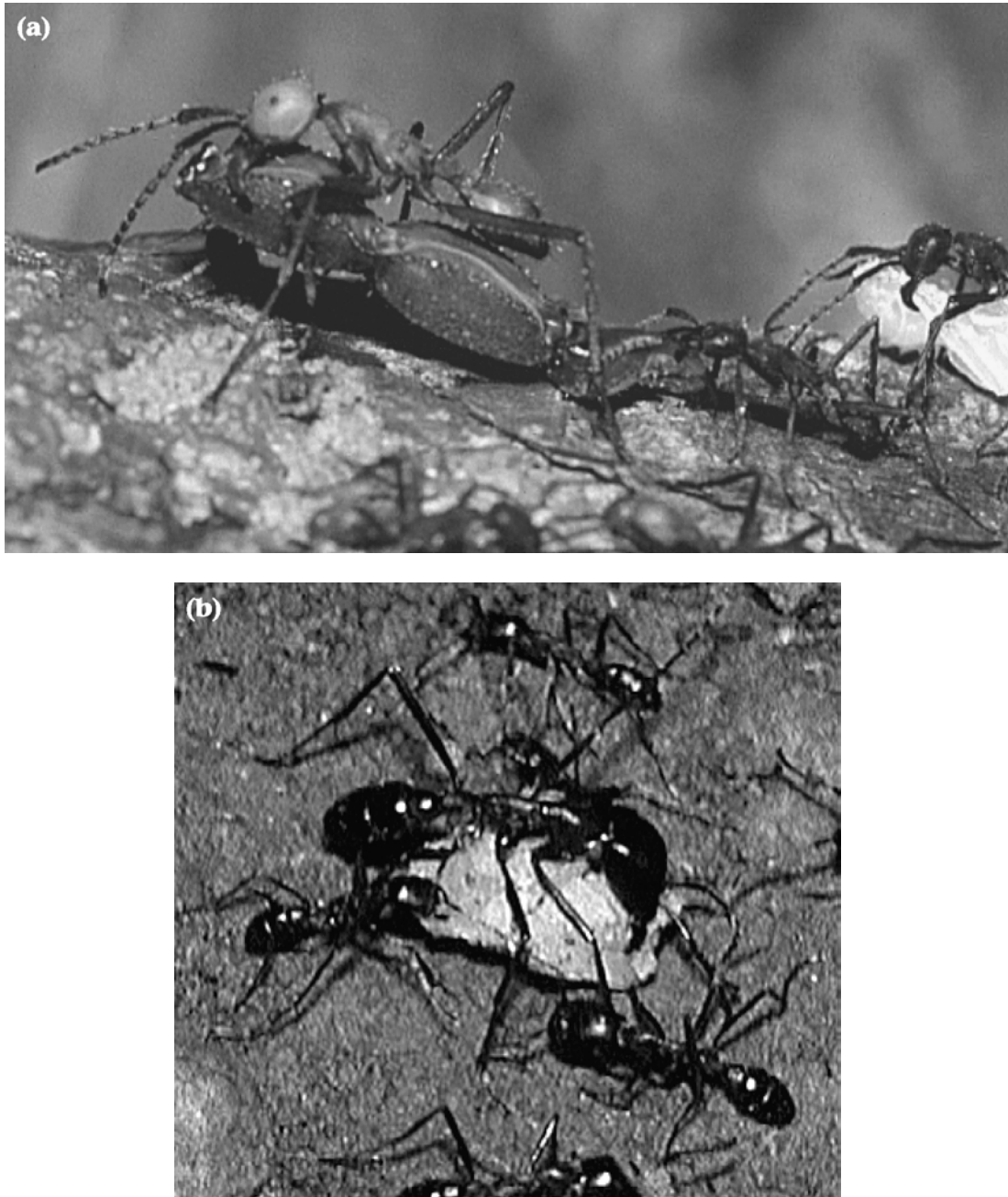
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Figure 1. (a) An *Eciton burchelli* team of two, retrieving part of a scorpion's tail; note the large submajor at the front and the small minor at the rear. (b) A *Dorylus wilverthi* team of two, retrieving an insect fragment; note the large worker at the front and the small one at the rear.

different castes or forms, the concept of teams can now be applied usefully to many other societies.

In studies of social insects, the issue of demonstrating different castes within groups can be problematic even when workforces are highly polymorphic. Social insect workers can be highly polymorphic, showing extreme size variation and different morphologies at the ends of the size range, yet exhibit such continuous size variation that discrete physical castes cannot be demonstrated (Hölldobler & Wilson 1990; Moffett & Tobin 1991). This is the case in the Old World army ant *Dorylus* (Hollingsworth 1960; Raignier et al. 1974). Nevertheless,

Dorylus wilverthi also forms superefficient prey retrieval groups that are comparable to those of *E. burchelli* (Franks et al. 1999).

Army ants are unusual in that they carry prey items by first straddling them so that they are slung underneath their bodies. This not only keeps the centre of gravity low but also enables two or more ants to carry the same item with both ants facing and pulling in the same direction (Franks 1986; Fig. 1).

The swarm raids of *E. burchelli* and *D. wilverthi* produce almost identical size distributions of prey items. In both cases, the tens of thousands of prey items in *E. burchelli*

and hundreds of thousands of prey items in *D. wilverthi* that are captured during a day's raid have to be retrieved considerable distances (Franks 1989; Gotwald 1995; Franks et al. 1999). The overall size range of workers in *E. burchelli* and *D. wilverthi* is also almost identical. However, the median size of workers in *D. wilverthi* is much smaller than that in *E. burchelli*: 98% of *D. wilverthi* workers are within the size range of the smallest 25% of *E. burchelli* workers (see Franks et al. 1999). In both species, the size distribution of workers has a long right skew but this is more pronounced in *D. wilverthi* and the distribution is not multimodal in *D. wilverthi* as it is in *E. burchelli*. (Franks et al. 1999). In *E. burchelli*, four discrete worker morphs can be recognized: majors, submajors, medium workers and minors (Franks 1985). In *D. wilverthi*, the workers show continuous variation (Raignier et al. 1974; N. R. Franks, personal observation). Many medium-sized to large prey items are carried by submajors in *E. burchelli*, which act as a specialist porter caste (Franks 1985). In *D. wilverthi*, however, workers of a similar size to *E. burchelli* submajors are comparatively rare. For this reason, Franks et al. (1999) predicted that there should be relatively many more prey retrieval groups in *D. wilverthi* than in *E. burchelli*. Such is the case. The proportion of all prey items retrieved by groups in *D. wilverthi* and *E. burchelli* is 39 and 5%, respectively, and the proportion of prey biomass retrieved by groups is 64 and 13%, respectively (Franks et al. 1999). Thus, prey retrieval groups have an important role in the foraging of both of these species of army ants.

Our goal in this paper is to understand better the division of labour that occurs within army ant teams. We also resolve a paradox: superefficient prey retrieval groups have been clearly demonstrated in *Dorylus* (Franks et al. 1999), but they cannot be considered teams according to earlier definitions (Hölldobler & Wilson 1990). To achieve these goals we examine the structure of prey retrieval groups in *Dorylus* in the light of the new definition of teams (sensu Anderson & Franks, in press) and we then use the same form of analysis in a comparative re-examination of the structure of prey retrieval groups in *Eciton*. Thus we determine if there is a nonrandom composition of members within prey retrieval groups in these Old and New World army ants that is consistent with Anderson & Franks' (in press) new definition of teams.

METHODS

Is the Front Ant the Largest Group Member?

We tested this hypothesis by examining photographs of prey retrieval groups in both *E. burchelli* and *D. wilverthi* taken in the field in Panama and Uganda, respectively. (For details of the field sites from which these data came see Franks et al. 1999 and references therein.) Such photographs (see for example Fig. 1) approximate an unbiased sample, because, at the running speed of such army ants, the composition of a prey retrieval group cannot be determined at the time that a photograph is taken. We used photographs for this part of the analysis because information on the relative positions of ants within a group is lost when the prey item is wrestled from them so that they and the prey item can be preserved for later determination of dry weights.

The photographic samples for *E. burchelli* were collected over an extended period of time during the 1980s from many colonies and all from Barro Colorado Island, Panama. The majority of these photographs were taken, however, during the same period and from the same colonies from which the preserved specimens were collected (Franks 1986). The photographic samples for *D. wilverthi* were collected during the same period of field study, as were the preserved specimens and from the same colonies in Kibale Forest, Uganda (Franks et al. 1999). Thus there is no reason, in either case, to suspect that there are any systematic biases between the photographed and collected specimens.

Henceforth, we refer to the ant at the front of each group as the front runner. This ant can be identified within a collected group because as the photographs reveal (see below) it is the largest ant within each group. All the other ants in the prey retrieval group (i.e. other than the front runner) we refer to as 'followers'.

Are Front Runners Unusually Large?

We tested the hypothesis that the front runner in each prey retrieval group is typically an unusually large worker among the ants present in raids. We used large samples of prey retrieval groups (for *E. burchelli* $N=106$ and for *D. wilverthi* $N=83$) collected in the field in Panama and Uganda that were processed as described in Franks (1986) and Franks et al. (1999). These samples were independent of the photographic samples described above. The distribution of nonprey-carrying raid workers in *E. burchelli* is based on a sample of 3314 ants (Franks 1985). Dry weights for these individuals are not available. However, they were sorted into four worker caste categories for which weight characteristics are known. The sample was 22% minims (less than 1.5 mg), 74.55% mediums (1.6–5.5 mg), 3.15% submajors (5.6–9.5 mg) and 0.3% majors (>9.6 mg). The continuous distribution shown in Fig. 2 in the Results and used for the statistical analysis was estimated by generating a normal distribution for each caste with a mean equal to the modal weight for that caste and a standard deviation of 25% of that mean. We used a two-tailed Wilcoxon rank-sum test (Lehmann 1975; Conover 1980) to examine differences between the dry weights of front runners and (1) nonprey-carrying raid workers, (2) the second-largest members of prey retrieval groups and (3) single porters.

Is Group Composition Nonrandom?

We used a Monte Carlo simulation model (a randomization test, Manly 1991) to test the hypothesis that prey retrieval groups in *E. burchelli* and *D. wilverthi* have a nonrandom composition of different worker sizes. Specifically, we tested whether the largest followers in the samples of prey retrieval groups collected in Panama and
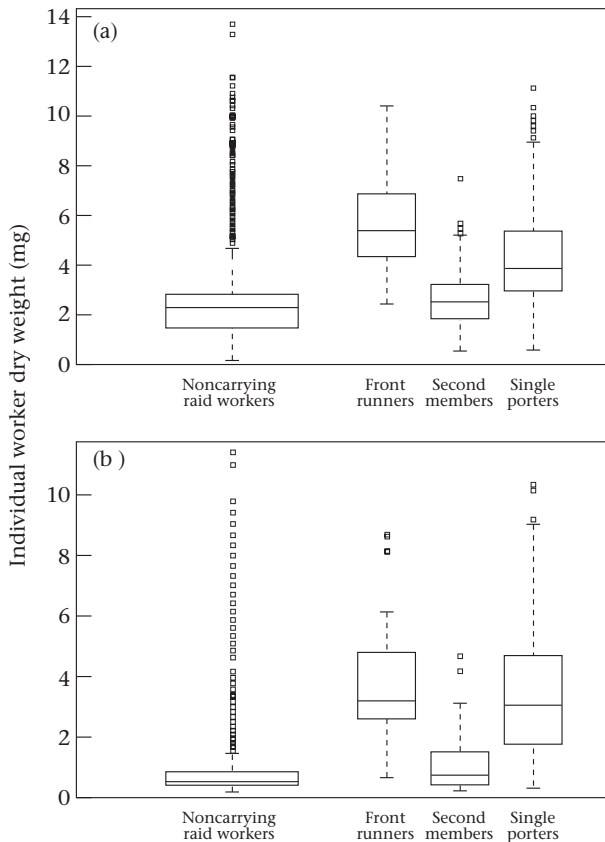
Figure 2. Box plots for the dry weight of nonprey-carrying raid workers, front runners in prey retrieval groups, second-largest members of prey retrieval groups and single porters sampled from a raid column of: (a) *E. burchelli* (Wilcoxon rank-sum tests: front runners versus nonprey-carrying workers: $Z=16.172$, $P<0.0001$; versus second-largest members: $Z=10.790$, $P<0.0001$; versus single porters: $Z=6.333$, $P<0.0001$); (b) *D. wilverthi* (Wilcoxon rank-sum tests: front runners versus nonprey-carrying workers: $Z=13.814$, $P<0.0001$; versus second-largest member: $Z=9.653$, $P<0.0001$; versus single porters: $Z=1.5056$, $P=0.132$). The width of each boxplot within each graph is proportional to the sample size; the box encompasses the interquartile range; the internal line is the median; whiskers are drawn to the nearest value within 1.5 times the interquartile range; squares indicate outlying points. For *E. burchelli*, the sample size for front runners and second-largest members is 106, for single porters 206 and for nonprey-carrying workers 3314. For *D. wilverthi*, the sample size for front runners and second-largest members 83, for single porters 125 and for nonprey-carrying workers 1754 (Franks et al. 1999).

Uganda are a random selection from the population of all sampled prey retrieval group members. Our objective was to compare the distribution of differences in weights between the largest and second-largest worker in such randomly assembled groups with the same distribution in the observed groups.

The simulation model was based on the following assumption: workers collected while retrieving prey were representative of the population of workers from which prey retrieval group members originated (i.e. the population of potential prey retrievers). This assumption was justified through the random sampling of large numbers of workers from raid columns of both species.

In the simulation experiment for *E. burchelli*, we estimated the population of potential prey retrievers by pooling single porters ($N=206$) and prey retrieval group members ($N=228$, hence total $N=434$) because there was no significant difference in the dry weight of individuals belonging to the single porter and the prey retrieval group populations (two-tailed Wilcoxon rank-sum test: $Z=1.484$, $P=0.140$). In the simulation experiment for *D. wilverthi*, the population of potential prey retrievers was estimated only from prey retrieval group members ($N=188$) because there was a significant difference in the dry weight of individuals belonging to the single porter and the prey retrieval group populations, the former being larger (two-tailed Wilcoxon rank-sum test: $Z=6.041$, $P<0.0001$).

The algorithm of the model was as follows.

(1) Record the heaviest member of the observed prey retrieval group. This is the front runner in that prey retrieval group. (As we show below the front runner can be recognized as the heaviest member of each prey retrieval group.)

(2) Record the total dry weight of the observed prey retrieval group.

(3) Calculate the total dry weight of followers by subtracting the weight of the front runner recorded in step 1 from the total dry weight of the group recorded in step 2.

(4) Randomly sample a follower from the population of potential prey retrievers, subject to the condition that her dry weight is smaller than the dry weight of the front runner and subtract the dry weight of that follower from the total dry weight of followers.

(5) Repeat step 4 (without replacement) until the total dry weight of the followers in the randomized group plus the front runner matches, or exceeds, the total dry weight of the observed prey retrieval group. Note that the population from which followers are sampled includes front runners from other groups.

(6) Calculate the dry weight of the largest worker in the randomized group of followers assembled in steps 4 and 5.

(7) Calculate the difference between the dry weights of the front runner and the largest worker among the randomized group of followers, that is, between the largest and the second-largest group members.

We followed steps 1–7 for each prey retrieval group in our samples ($N=106$ for *E. burchelli*; $N=83$ for *D. wilverthi*). We then calculated the median for the distribution of the differences between the dry weights of the largest and the second largest workers in the prey retrieval group for the 106 values for *E. burchelli* or the 83 values for *D. wilverthi*. For each of the two species we then iterated this whole procedure another 499 times (with replacement). Thus for each species we generated a distribution of 500 median values, against which we could compare the observed value of the same statistic, namely the median of the distribution of differences between the dry weights of the largest and second-largest worker in the prey retrieval groups with the observed composition of different worker sizes.

Team Replacement Experiments

Experiments that involve taking prey items away from teams and replacing them in foraging columns so that a new team forms around the item give some insight into team formation (Franks 1986; Franks et al. 1999). In such experiments, we determined the dry weights of every member of the initial team and of every member of the replacement team as well as the dry weight of the prey item that was taken from the first team and replaced in the foraging column so that another team could form around it. We did 20 such experiments with *D. wilverthi* and 32 with *E. burchelli*.

RESULTS

Is the Front Ant the Largest Group Member?

We had photographs of 39 *E. burchelli* prey retrieval groups. In this sample 82% of groups had only two members. (This is comparable to the 88% of *E. burchelli* prey retrieval groups only having two members as reported by Franks 1986 from a larger sample size of unbiased observations.) In the photographic sample, prey retrieval groups of three or more were too few ($N=7$) to analyse statistically and in four of the groups of two workers the front runner and the second ant appeared of similar size. This left 28 prey retrieval groups with two participants of recognizably different size. In all of these cases, the ant at the front was the larger of the two ($\chi^2_{corr1}=26.04$, $P<0.001$, one tailed). (χ^2_{corr1} refers to Yates' correction for continuity, see Sokal & Rohlf 1969.)

A total of 23 *D. wilverthi* prey retrieval groups were photographed. In this sample, 91% of the prey retrieval groups had only two members. (This is similar to the 81% of all *D. wilverthi* prey retrieval groups having only two members from a larger sample size of unbiased observations as analysed by Franks et al. 1999) In the photographic sample, prey retrieval groups of three or more were too few ($N=2$) to analyse statistically and in two groups of two workers the front runner and the second ant appeared of similar size. This left 19 prey retrieval groups with two participants of recognizably different size. In all of these cases, the ant at the front was the larger of the two ($\chi^2_{corr1}=17.05$, $P<0.001$, one tailed).

Hence, in both species, the front runner was the larger ant in a group. In prey retrieval groups of more than two this also always appears to be the case (personal observations), but the smaller sample sizes of photographs of such larger prey retrieval groups precluded a statistical analysis.

Are Front Runners Unusually Large?

Front runners in prey retrieval groups were unusually large workers. Their dry weight was significantly greater than that of workers in raids that were sampled when not carrying prey. This was the case in both *E. burchelli* (Fig. 2a) and *D. wilverthi* (Fig. 2b). Furthermore, in *E. burchelli*, the dry weights of front runners were also significantly greater than those of single porters of prey (Fig. 2a).

Is Group Composition Nonrandom?

Typically, the second-largest worker in a prey retrieval group was especially small. The randomization tests show that, in both *E. burchelli* (Fig. 3a) and *D. wilverthi* (Fig. 3b), the median difference in dry weight between the largest and the second-largest worker in a prey retrieval group was significantly greater than that expected if the front runner was equally likely to be joined by any ant or ants from the population of potential prey retrievers.

Team Replacement Experiments

In each of these experiments a cluster of ants was observed to form around the large stationary prey item that had been taken away from the first team and replaced in the foraging column. Eventually, a sufficiently large ant was seen to get the item into motion. In this way, large prey items 'select' an unusually large first ant because only such an ant can begin to move the item. This big ant becomes the ant at the front of the team, that is, the front runner. In *Eciton*, in 56% (i.e. 18) of the 32 trials a single ant, which in 89% of the cases was a submajor, carried off the item unaided, replacing the efforts of two ants of similar (combined) weight. In *Dorylus*, a single ant replaced the initial team in only one of the 20 trials. During the formation of a new team, in both species, one or more ants joined in to help the front runner until the item was being carried at the species-characteristic standard prey retrieval speed (Franks et al. 1999). At such a speed, the item no longer interrupts smooth traffic flow and it is no longer a stimulus for other ants to join in the group retrieval (Franks 1986).

In both *Eciton* and *Dorylus*, there is a strong correlation between the total dry weight in the original team and the dry weight of the ants or ant that replaced it (*E. burchelli* $r_{30}=0.70$, $P<0.001$; *D. wilverthi*: $r_{18}=0.80$, $P<0.001$). In both species, there is a significant positive correlation between the dry weight of the front runner in the original team and the weight of the front runner in the replacement team (*E. burchelli*: $r_{12}=0.56$, $P<0.05$; *D. wilverthi*: $r_{17}=0.70$, $P<0.001$), but no statistically significant correlation between the dry weights of the second-largest workers in the original and replacement teams (*E. burchelli*: $r_{12}=0.22$, NS; *D. wilverthi*: $r_{17}=0.37$, NS).

DISCUSSION

In both *E. burchelli* and *D. wilverthi*, the analysis of prey retrieval group composition, presented for the first time in this paper, showed that the largest ant in a prey retrieval group is typically from the right-hand tail of the size distribution, and is therefore unusually large. The randomization tests showed that the second-largest ant in these prey retrieval groups is surprisingly small. That is, the second ant in a prey retrieval group is much smaller than expected if it had been picked at random from the size distribution of potential prey retrieval group workers. These findings clearly show that both Old World and New World army ant prey retrieval groups have a definite
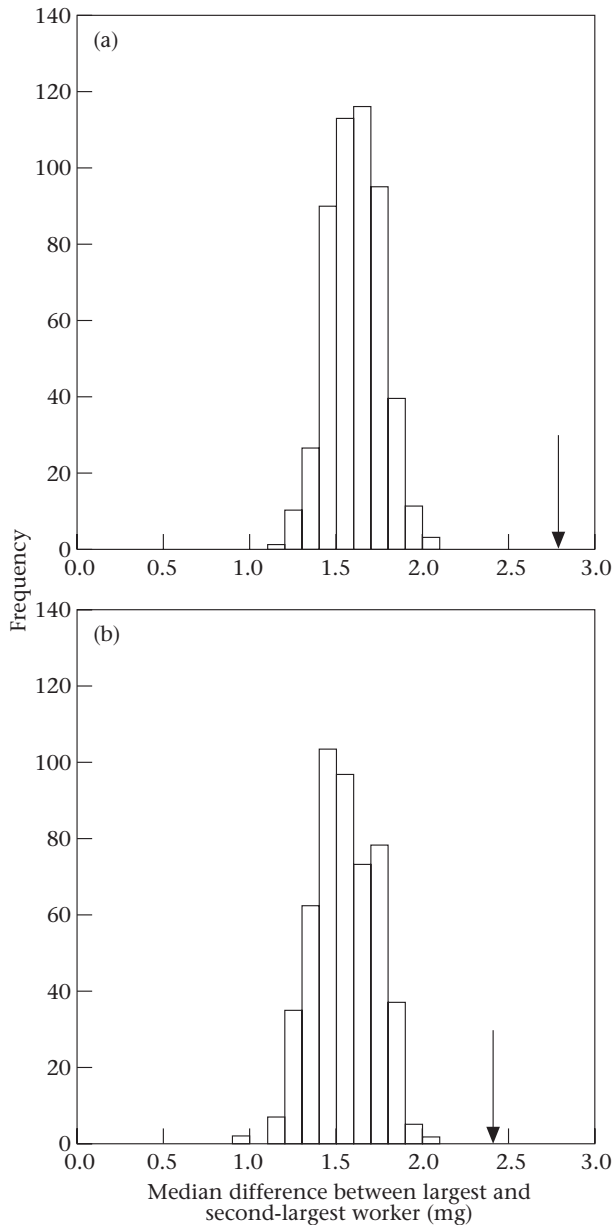
Figure 3. Results from the randomization tests of the null hypothesis that the dry weight of the second-largest worker in a prey retrieval group is not significantly different from that expected if followers from the population of potential prey retrievers are equally likely to join the front runner in (a) *E. burchelli* and (b) *D. wilverthi*. The arrows (at 2.78 mg for *E. burchelli*, N=106; at 2.40 mg for *D. wilverthi*, N=83) indicate the value of the median of the distribution of the difference between the dry weights of the front runner and the second-largest worker for each of the observed data sets for prey retrieval groups. The histograms represent the frequency distribution of such a median for 500 randomized data sets for prey retrieval groups. Each randomized data set was generated by combining each front runner from the observed data set (N=106 for *E. burchelli*; N=83 for *D. wilverthi*) with a set of followers taken at random from the population of observed prey retrievers (N=434 for *E. burchelli*; N=188 for *D. wilverthi*). The observed value of the median is the highest among the 501 such values sampled at random from all possible values of this statistic. The null hypothesis can, therefore, be rejected at the probability level of P=1/501=0.002.

structure with a very large size disparity between the largest and second-largest ant in the teams. This structure strongly suggests that there are different task requirements in the different spatial positions within a prey retrieval group. Thus there is a division of labour consistent with the Anderson & Franks (in press) definition of teams. Hence prey retrieval groups in both *Eciton* and *Dorylus* should be referred to as teams.

Is the observation that the second-largest ant is unusually small the result of an active or passive process that matches the size of the worker to the size of the task? It would be active if workers that were too large actively avoided joining teams in which they would not be fully employed (see for example, Wilson 1985). It would be passive if small workers became involved more often simply by default because larger workers were comparatively rare. The data, at least for *Eciton*, suggest that the process is an active one. In *E. burchelli*, single very large workers substituted 44% of the teams in the replacement experiments. Furthermore, in both species in these experiments large front runners rapidly took up the replaced prey items. This suggests that large workers are sufficiently abundant quickly to become single retrievers, front runners or followers. This implies that the second-largest ants in teams are small not because only small ones are available but because large ants choose not to become employed in this way. That is, if an unnecessarily large ant tries to help a front runner and finds that the remaining work is too slight to employ her full efforts she does not join the team. One or more much smaller ants whose efforts are fully employed become involved instead.

Future work on *Dorylus* and many other foraging ants should try to determine if task/size matching is an active or a passive process. This would help to test an important principle in the division of labour: specialized individuals should not allow themselves to be inappropriately employed in tasks that would prevent them from seeking more suitable tasks. In solitary foragers in other animals, it is often the variance in food item size that increases with forager size, as well as the mean, that is, larger foragers can capture larger prey, but still capture small prey too (see for example, Hop et al. 1993; Webb et al. 2000). In social foragers in which there is size variation as in the case here, larger individuals may sometimes leave these smaller prey to their smaller companions (but see Horstmann 1973). Such a division of labour would probably lead to greater overall efficiency.

The formation of army ant teams is also an example of tasks allocating workers rather than workers allocating tasks (see Franks & Tofts 1994; Bourke & Franks 1995). The observations from the team replacement experiments, especially on *Eciton*, further emphasize this point. Presumably, the single workers that replaced teams in 18 out of 32 trials could run at the standard retrieval speed; hence, no other worker was stimulated to join in. In both *Eciton* and *Dorylus* the correlation between the total dry weights of teams and their replacement teams is positive and significant but it is not perfect. The correlation between the front runner in such teams and replacement teams is also positive and significant but it is weaker.

Why? The total team weight probably largely dictates the retrieval speed and this must match the standard retrieval speed. The dry weights of front runners in teams and their replacement match but do so more weakly because the only requirement is that both of these front runners must be able to get the item into motion alone. There is no significant correlation between the weights of the second-largest members of such teams and replacement teams because the second-largest ant has an even weaker requirement for matching; all it has to do is help to some extent. If it does not help sufficiently to bring the prey item up to the standard retrieval speed a third ant will join the team and so on.

It is also clear that efficient teams should not stay together after their work is done, that is, they do not come and go as teams. Indeed, Oster & Wilson (1978, page 151) originally dismissed the possibility that teams occurred in social insects partly because they thought of such teams as having a constant membership. In army ants, team tasks vary too much, in terms of the number and sizes of ants needed to move a large prey item, to warrant permanent teams. Such teams would spend much more time searching for an appropriate task than being productive. There is a very strong correlation between prey weight and team weight, so a permanent team of a certain weight would have to search for a long time for the exact prey item to match their strengths.

One might argue that although radically different sizes of ants form army ant teams, each has the same subtask but this is extremely unlikely. The front runner gets the prey item in motion and carries most of the weight. It presumably steers and determines the direction that the team will take. The supplementary ant (or ants) then joins the front runner and follows it. Such followers, being so small, almost certainly carry much less weight than the front runner. Working together, the front runner and its follower(s) bring the velocity of the prey item up to the standard retrieval speed of the foraging column (Franks 1986; Franks et al. 1999). They are able to work superefficiently probably because by straddling the prey item between them its rotational forces are balanced and disappear (Franks 1986). Both the front runner and the follower(s) will contribute to the removal of rotational forces, but the second ant initiates this process when it joins the front runner. Indeed, when the front runner first starts to move a large item it must combat all of the rotational forces. The second ant relieves the first of much of this effort when it begins to work concurrently with the front runner.

To help illustrate the difference in subtasks between the front runner and a follower, consider a penny-farthing bicycle. Such bicycles were locally common in the latter part of the 19th century (see Fig. 4). They have a very big wheel at the front and a tiny one at the rear. The diameter of the front wheel is often three, or more, times greater than that of the rear wheel. Like an army ant team of two the load-bearing device at the front is very large and the one at the rear is very small. Like the army ants the one at the front is the (main) driving wheel and the one at the rear prevents the system toppling backwards and forwards. The back wheel of a penny-farthing endows the
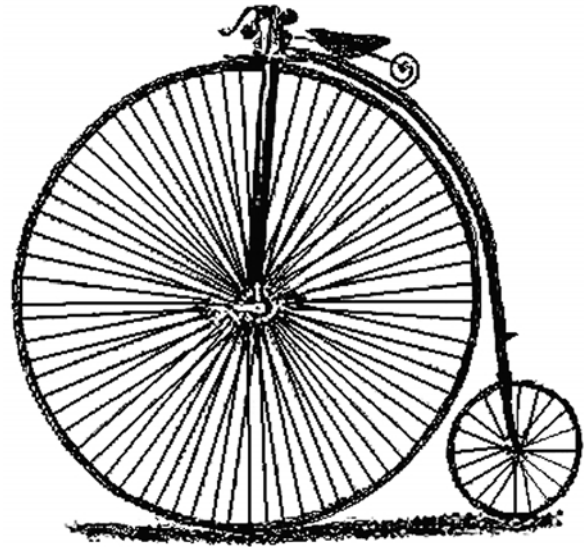

Figure 4. A penny-farthing bicycle (19th century).

machine with very different properties to a unicycle. The rider of a penny-farthing sits (slightly) behind the axle of the front wheel, not over it. Hence as in army ants rotational forces are balanced and disappear. It is very clear that the two wheels on a penny-farthing have different subtasks. The front wheel takes most of the load, drives the system forwards, and steers. All of this is very likely to be true of an army ant team of two.

The analogy with a penny-farthing bicycle reveals how a team of two can be more than the sum of its parts. The tiny castor-like wheel on a penny-farthing transforms the properties of the machine out of all proportion to its size. Similarly, the synergism between a large ant and a small one in a team boosts the performance of both, again because rotational forces are balanced and disappear.

The new definition of teams by Anderson & Franks (in press) focuses upon the concurrent performance of different subtasks. The term concurrent is used in the definition rather than simultaneous because the former does not imply synchronized starting or finishing. Certainly, in army ants a team does not start its work in synchrony; supplementary ants join in only if their efforts are needed. This new definition invokes different subtasks rather than different castes, as in the old Hölldobler & Wilson (1990) definition. This is preferable, first, because the occurrence of different castes in a team implies the occurrence of different subtasks and, second, because different subtasks may be performed by members of the same caste. Therefore, investigations of possible teams should focus on whether there are different (concurrent) subtasks. Our use of randomization tests shows how structured patterns of subtasks can be demonstrated or strongly inferred from behavioural or size-related data.

Further progress in understanding the organization of work in insect societies is likely to be made by considering what tasks and subtasks workers perform rather than

putting too much emphasis on attempts to classify workers into discrete caste categories.

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