

The emergence of division of labour in forced associations of normally solitary ant queens

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ABSTRACT

We tested the hypothesis that division of labour is an inescapable property of social groups, rather than an evolutionary event separate from sociality. We propose a variance-based emergent property model in which division of labour can spontaneously emerge when (1) individuals in a group vary in their intrinsic sensitivity to stimuli for a given task, and (2) the performance of a task by individuals with higher task sensitivities reduces performance of the task by the other group members. Under these conditions, the individuals with higher sensitivity become the task specialists. To determine if division of labour can occur in the absence of direct selection, we created artificial foundress associations (groups of queens during nest establishment) of the ant *Pogonomyrmex barbatus*, which has no history of cooperative colony founding. We compared the incidence of task specialization in this species to that in *Pogonomyrmex californicus*, in which foundress associations commonly occur. Levels of task specialization for nest excavation were high in both species, arguing that division of labour emerges in groups regardless of evolutionary history. Consistent with the variance-based model, the role of nest excavation specialist in *P. barbatus* foundress associations could be predicted by both (1) differences in excavation roles in prior pairs and (2) variation in excavation activity while solitary. Furthermore, the assumption of the excavator role by one foundress dramatically reduced the performance of that task by the other foundress of the pair. We also found a strong negative relationship between excavation activity and foundress survival in *P. barbatus*, suggesting that division of labour in this context may act as a constraint on social evolution.

Keywords: division of labour, emergent properties, foundress associations, *Pogonomyrmex barbatus*, self-organization, social insects, task specialization.

INTRODUCTION

Division of labour, where individuals within a group specialize on different tasks, is considered one of the primary adaptations of sociality (Wilson, 1971; Szathmary and Maynard Smith, 1995). The traditionally accepted model for the origin of division of labour is via selection for task specialization after the formation of social groups (Oster and Wilson, 1978; Wilson, 1985a,b; but see also West Eberhard, 1987). However, the question of how

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task specialization evolves within social groups is still unresolved. In kin groups, selection on the queen can theoretically produce task specialization in workers. However, the mechanism by which this occurs is not clear. Furthermore, kin selection cannot explain the similar patterns of task specialization among individuals in groups of unrelated individuals. In this paper, we explore the alternative hypothesis that division of labour does not originate directly via mutation and selection, but instead is an inescapable emergent property of groups in which there is behavioural variation among individuals.

A plethora of research has shown that task specialization in complex social units is based in part on intrinsic variation among workers (Calderone and Page, 1988, 1991; Frumhoff and Baker, 1988; Robinson and Page, 1989; Stuart and Page, 1991; Oldroyd *et al.*, 1992; Snyder, 1993; O'Donnell, 1996). However, it is unclear how this relationship was established evolutionarily (before or after the evolution of sociality), or how fundamentally it contributes to division of labour. In a model of honey bee social organization, Page and Mitchell (1991) suggested that this variance is central to task organization, and that task specialization within honey bee colonies self-organizes from intrinsic variation among members in their probabilities of performing different tasks.

From the model of Page and Mitchell (1991), we can extrapolate that division of labour should emerge in all social groups in which the following general conditions occur: (1) individuals in a group vary intrinsically in their tendency to perform a behaviour, and (2) the behaviour once performed changes the social environment, reducing the stimulus for that task. Under these conditions, performance of a task by individuals with higher intrinsic sensitivities to task stimuli reduces the need for that task, so that other members of the group perform the task at lower levels than they would if solitary. As a result, the individual performing the task becomes the task specialist.

This variance-based emergent property model generates several testable expectations. First, if task specialization is an emergent property of social groups, regardless of their evolutionary history, then task specialization can occur in groups with no history of selection for division of labour. Second, if task specialization is based on intrinsic variation among the members of the group, we should be able to predict which individual in a group becomes the task specialist based on (1) their differential performance of that task in previous groups, or (2) their performance of the behaviour when solitary. Third, if task specialization is truly an emergent property, the probability of task performance must encompass an interaction effect of being in a social group and not be a simple summation of variance in task preference among individuals. Specifically, in a group with a task 'specialist', the other individuals should reduce performance rates below those which occur when they are solitary or paired with an individual with a lower tendency to perform the task. We would also expect that task specialization will emerge across social groups, even when it requires individuals in the group to change roles from other social contexts.

Because our model specifically predicts that division of labour will arise without selection, we needed to test it in a context without a history of direct selection. We created incipient social groups from traditionally solitary individuals by generating artificial foundress associations in the ant *Pogonomyrmex barbatus*. In most ant species, including *P. barbatus*, nests are initiated by a solitary female. However, in some species, groups of mated females initiate nests together (Hölldobler, 1976a,b; Hölldobler and Wilson, 1977; Bartz and Hölldobler, 1982). In the polygynous species that have been tested (*Messor pergandei* and *Acromyrmex versicolor*), these foundress associations demonstrate task

specialization during nest construction, with one foundress becoming the principal excavator (Rissing and Pollock, 1986; S.W. Rissing and J.H. Fewell, unpublished data).

We compared levels of task specialization in the artificial *P. barbatus* foundress associations with those of *P. californicus*, the only *Pogonomyrmex* species known to form foundress associations in the field. We would expect that if task specialization requires selection, then levels of task specialization would be considerably lower in *P. barbatus* than in species with an evolutionary history of foundress associations. In contrast, if division of labour is an emergent property, we would expect to see similar levels of task specialization across these species. We also tested the other expectations of the variance-based model by observing the behaviour of individual *P. barbatus* foundresses under solitary conditions and in associations in which they would be expected to retain or change roles depending on the social context.

METHODS

Experiment 1: Excavation behaviour in *P. barbatus* and *P. californicus*

We collected newly mated *P. barbatus* queens from Portal, Arizona, in the early evenings of 20 and 23 July 1994. Extensive surveys of this population have found no evidence of nest co-founding by this species (Hölldobler, 1976a; R. Johnson, personal communication). Collected queens had shed their wings and were walking along the ground, but had not yet begun nest excavation. The ants were placed into individual eppendorf tubes and immediately transported to Arizona State University, where they were weighed, individually marked with paint on the abdomen and placed in pairs into 250 ml bottles containing soil from the locality of the collection site. Pairs were observed beginning immediately after set-up for 40 min each hour. We recorded each excavation event, consisting of digging in the soil or carrying soil away from a nest entrance. We performed this experiment in two replicates. In the first replicate, we observed 41 foundress pairs over 22 h. We found that all pairs reached the bottom of the chamber before 20 h and that behavioural asymmetries seen in the first 8 h were not reversed through the rest of the observation period. Therefore, we observed our second replicate of 22 pairs over 8 h.

We conducted the same experiment on *P. californicus* foundresses collected from San Diego county, California in June, using parallel methods to those for *P. barbatus*. Queens of this population form foundress associations of up to 30 individuals (R. Johnson, personal communication). We set up 50 pairs, which we observed for 45 min each hour over a 22 h period. We analysed each pair of *P. barbatus* and *P. californicus* using χ^2 to determine whether the two foundresses excavated with statistically different frequencies.

Experiment 2: Persistence of excavation roles across *P. barbatus* pairs

In this experiment, we tested the predictions that (1) task roles within associations can be predicted from intrinsic differences between foundresses, and (2) asymmetries in task performance will occur across foundress associations, even when one foundress must shift roles for asymmetry to occur. Foundresses from each *P. barbatus* pair in Experiment 1 that showed asymmetry in excavation behaviour were categorized as high-frequency excavators (HFE) or low-frequency excavators (LFE) based on their relative excavation frequencies.

We removed the foundresses from these pairs and placed them into new associations in bottles containing fresh soil. We set up three types of pair associations consisting of: (2a) both foundresses previously HFE (17 pairs), (2b) both foundresses previously LFE (17 pairs), (2c) one foundress previously HFE and the other previously LFE (19 pairs). Pairs were set up and experiments begun immediately after the completion of Experiment 1. All pairs were observed for 30 min each hour for 8 h.

Experiment 3: Relationship between solitary behaviour and task role in foundress associations

We also considered whether the roles of high-frequency and low-frequency excavators could be predicted from the behaviour of *P. barbatus* foundresses as solitary individuals. Concurrently with Experiment 1, we placed 18 marked foundresses (with no prior excavation experience) individually into 250 ml bottles. We observed these foundresses for 40 min per hour for 22 h. All of the ants dug, but they varied in excavation frequency. We divided the group of 18 foundresses into two sets, based on excavation frequency, then paired the more frequent excavators with the less frequent excavators in new chambers. To create pairs that differed in excavation activity, the queen with the lowest excavation rate in the first (lower rate) group was paired with the lowest excavation rate in the second (higher rate) group, and so on. These pairs were observed for an additional 8 h, and excavation frequencies of each foundress in the pair scored. The bottles were maintained after the experiment until most foundresses produced worker offspring. We took the nests apart on 22 September, 2 months after the excavation experiment, and identified which foundresses survived.

RESULTS

Does excavation behaviour vary between *P. barbatus* and *P. californicus*?

The emergent property model makes the prediction that task specialization should occur across most pairs in both species. In contrast, if division of labour in *P. californicus* foundress associations is primarily an evolved response to selection, then levels of task specialization should be extremely low in *P. barbatus* relative to *P. californicus*. Excavation behaviour occurred in all bottles for *P. barbatus* at levels sufficient for analysis, but we excluded four pairs of *P. californicus* because of inadequate levels of excavation behaviour (<10 excavation trips in total). We also excluded all pairs for both species in which one foundress did not excavate, in the unlikely case that she was injured (although these queens were generally healthy later in the experiment) or physically unable to excavate. This eliminated 24 of 63 *P. barbatus* pairs and six of 50 *P. californicus* pairs from analysis. In both *P. barbatus* and *P. californicus*, most pairs showed significant asymmetry (χ^2 , $P < 0.05$) in excavation behaviour (Fig. 1). Despite the elimination of a number of obviously asymmetrical pairs from the *P. barbatus* group, that species still showed higher levels of task asymmetry than *P. californicus* ($\chi^2 = 5.3$, $P < 0.05$; Fig. 1).

The *P. californicus* pairs began excavating soon after being placed in the bottle. However, either one or both *P. barbatus* foundresses often remained still for a few hours after the experiment began. This was clearly not a result of injury. These foundresses often moved past the excavating queen into the nest after it was sufficiently deep to conceal the foundress.

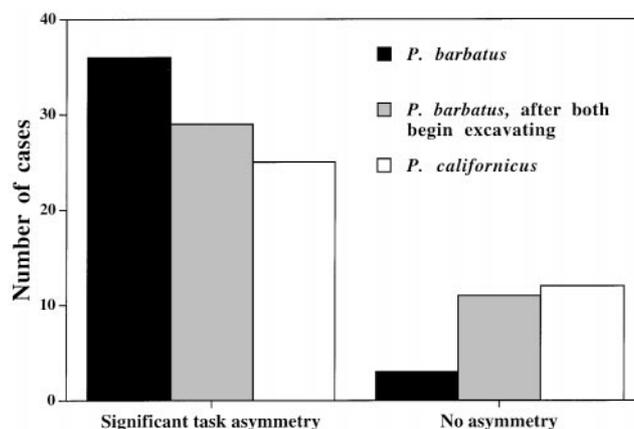


Fig. 1. The number of pairs in which foundresses showed significant asymmetries in excavation behaviour (χ^2 , $P < 0.05$) for *Pogonomyrmex barbatus*, *P. barbatus* (excavation data after both foundresses began to excavate) and *P. californicus*. Only pairs in which both foundresses excavated were included in the analysis.

Furthermore, many of these queens excavated (usually at low levels) later in the experiment. To compare excavation behaviour independently of the difference in latency period, we also calculated *P. barbatus* excavation rates only for pairs in which both individuals excavated, and only for that portion of time after the second foundress to excavate performed the behaviour. When we did this, the proportion of asymmetrical pairs was similar for the two species ($\chi^2 = 0.22$, $P = 0.6$; Fig. 1).

Do task roles persist across pairs of *P. barbatus*?

If task asymmetries are driven by intrinsic variation in task preference, we would predict that individuals would retain their roles of HFE or LFE if paired with an individual that previously held the other role. In 16 of 19 cases in which *P. barbatus* foundresses previously categorized as HFE were paired with unfamiliar foundresses that were previously LFE, the two foundresses retained the roles they had in the first association (in two cases the roles were reversed, one was non-significant).

The model generates the expectation that task specialization should emerge across new associations even when foundresses in the new association held similar roles in prior pairs. Significant asymmetries occurred in 15 of 17 cases in which two previously HFE foundresses were paired, and in all 17 cases in which previously LFE foundresses were paired.

We predicted that performance of the task by one individual reduces the rate of its performance by other individuals. In all new pair sets (both HFE, both LFE, and HFE paired with LFE), foundresses in the LFE role had dramatically lower excavation rates than the principal excavator (Fig. 2). For this to occur in the HFE–HFE and LFE–LFE pairs, one of the two foundresses either decreased (HFE) or increased (LFE) excavation rates from their previous pair.

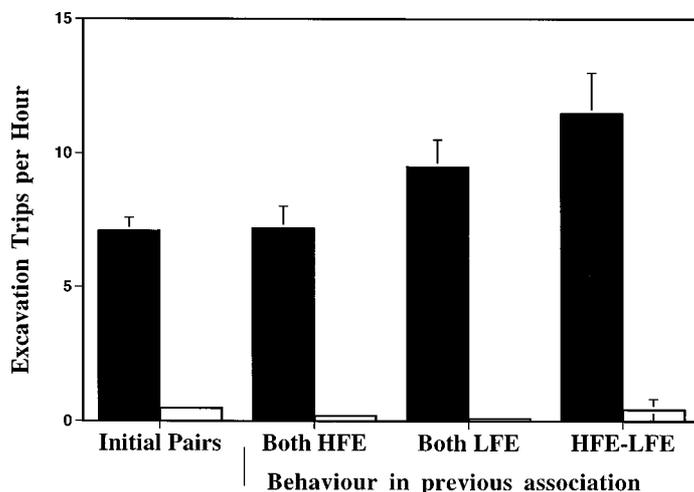


Fig. 2. Excavation rates (number of excavation trips per hour) for the foundresses that excavated more frequently versus the foundresses with lower excavation rates in the foundress pairs of Experiment 2. Pairs consisted of: (1) both foundresses previously HFE, (2) both foundresses previously LFE, (3) one foundress previously HFE and the other foundress previously LFE. The graph also shows excavation frequencies for the original pair sets, in which neither foundress had previously excavated (Experiment 1). However, direct comparisons of excavation rates between Experiment 1 and subsequent pairs are complicated by different observation times and a different number of chambers being observed simultaneously. ■, high-frequency excavator; □, low-frequency excavator.

Can excavation roles be predicted from the behaviour of solitary foundresses?

The model also makes the prediction that the roles of LFE and HFE can be determined from the relative task performance of foundresses when solitary. The 18 solitary foundresses that we observed varied in excavation rates. The number of excavation trips over the 22 h period ranged from 4 to 109 (mean \pm s.e. = 56.8 ± 7.75). Differences in individual excavation rates were consistent with the behaviour of the foundresses in pairs. In eight of the nine pairs, the foundress that excavated more frequently when solitary (HFE) excavated significantly more frequently than the other foundress of the pair (χ^2 , $P < 0.05$). The ninth pair showed a similar but non-significant trend. This experiment also provided an additional test of the expectation that the performance of a task by the HFE individual will reduce its performance by the other member of the group. The excavation rates of HFE foundresses did not vary significantly from solitary to pairs (paired t -test; $t_8 = 0.55$, $P > 0.50$), but the LFE excavators had significantly lower excavation rates in pairs than they did as solitary foundresses ($t_8 = 3.08$, $P = 0.01$; Fig. 3).

How does excavation behaviour relate to foundress survival?

We compared foundress excavation roles to the probability of survival in the two experiments in which we predicted foundress roles to remain constant. These were Experiment 2c, in which HFE queens from our first experiment were paired with unfamiliar LFE queens, and Experiment 3, in which solitary foundresses were placed in pairs. In both experiments,



Fig. 3. Excavation rates (excavation trips per hour) for foundresses that were placed individually into chambers, and then into new chambers in pair sets (Experiment 3). Data shown compare excavation rates for foundresses that became HFE in pairs with those that were LFE in pairs. ■, high-frequency excavators (while solitary); □, low-frequency excavators (while solitary).

foundress survival was linked negatively to excavation behaviour. There were eight cases in Experiment 2c in which one queen (as opposed to both or neither) survived. In seven of these cases, the survivor was the LFE. Of the nine pair sets in Experiment 3 (solitary to pairs), eight had only one surviving queen 2 months after the experiment. In seven of these eight cases, the surviving queen had been the LFE in the pair (binomial test, $P < 0.05$).

DISCUSSION

Our results provide strong evidence that task specialization is an emergent property of sociality. Intrinsic differences in nest excavation behaviour between foundresses led to the emergence of strong task specialization within these artificially induced social groups. The frequency of excavation specialization was extremely high in *P. barbatus*, a species with no demonstrated natural occurrence of foundress associations. Task specialization in these forced associations equalled or surpassed that seen in *P. californicus*, a species in which queens cooperatively build nests in the field. Levels of task specialization in these two species (approximately 70% of pairs) were also similar to that seen in *Messor pergandei* (S.W. Rissing, unpublished data), a species in which foundress associations are almost universal. Our results are inconsistent with a classic model in which task specialization evolves after the evolution of sociality, and instead suggest that division of labour is an inescapable property of social groups.

Given that some ant species show cooperative colony founding, we need to consider carefully the possibility that *P. barbatus* maintains an unexpressed genetic propensity for this behaviour from associations in its evolutionary past. Foundress associations are the exception rather than the rule in ants (Hölldobler and Wilson, 1977). Of the approximately

25 North American species within the *Pogonomyrmex* genus, only *P. californicus* has been reported to found nests cooperatively (Rissing *et al.*, in press). The *californicus* complex is taxonomically well removed from *P. barbatus* (Taber, 1990). Within the *barbatus* complex, *P. rugosus*, *P. desertorum*, *P. apache* and *P. bicolor* are reported to found nests individually (Cole, 1968; Hölldobler, 1976a; R. Johnson, personal communication). Therefore, it is extremely unlikely that *P. barbatus* have evolved, but then secondarily lost, cooperative colony founding.

Division of labour has traditionally been viewed as an adaptive component of sociality. However, in the case of *P. barbatus*, task specialization within foundress associations was clearly not mutually beneficial. In most cases in which we could track the relationship between excavation role and survival, the surviving queen was the *non-excavator*. The predictable negative relationship between excavation specialization and queen mortality argues against a history of selection for co-founding in *P. barbatus*, and instead generates the expectation that selection would drive the system towards a lower incidence of specialization. Thus, division of labour in this context may actually act as a constraint on social evolution.

Task specialization and the potential for social parasitism

The strong relationship between variation in task performance and reproductive advantage (becoming the queen) in *P. barbatus* can also be considered from the perspective of a potential mechanism for social parasitism. In our experiments, one foundress clearly gained a reproductive advantage through a reduction in work output, at the expense of the other. However, this advantage was not produced via selection for a specific parasitism 'strategy', suggesting that social parasitism, like division of labour, can occur from social interaction effects in the absence of selection.

If social parasitism can emerge so easily in incipient groups, how do those species with evolved foundress associations manage to maintain sociality? Evidence suggests that the potential for 'cheating' in evolved foundress associations has been reduced. Although we were unable to obtain mortality data on *P. californicus*, we have found no correlation between task performance and probability of mortality in *Messor pergandei*, which are almost obligate in their formation of foundress associations (J.H. Fewell and S.W. Rissing, unpublished data). The reduced levels of task specialization in *P. californicus* and *M. pergandei* suggest that the potential for social parasitism is countered in part by reduced variation in task performance among foundresses. However, the following questions remain unanswered: (1) Why is reduced variation within some groups selected for instead of selection away from sociality? (2) What other potential mechanisms act in these species to counter cheating?

Intrinsic variation and the emergence of task specialization

Our results strongly support the expectation of the variance-based model that task specialization is generated from intrinsic variation in task preference. We were able to successfully predict which *P. barbatus* queen would become the excavator specialist in a pair based on their relative task performance in prior groups. Individuals identified as the HFE in initial pairs retained that role in new associations in which they were paired with a previous LFE. We could also predict which individual in a pair would become the HFE based on their

relative excavation behaviour as solitary foundresses. These data support the assertion that division of labour can be generated from variance that individuals bring into a social group from a solitary context. With no change in the rules of behaviour from solitary to social, individual interactions with the social environment change the probability of individual task performance, generating division of labour.

Our data also support the expectation that task specialization emerges across social groups that show some behavioural variance. In the cases where we paired HFE–HFE individuals and LFE–LFE individuals, task asymmetries again emerged, even though we compressed the potential variance in behaviour by pairing two individuals that previously occupied similar roles. Emergence of task specialization in these pairs also required the assumption of new roles by one of the pair members, demonstrating that task specialization in this case was a property of the group rather than a fixed property of the individual members.

Finally, our results show that task performance by one individual can alter the social environment sufficiently to change the behavioural repertoires of others in the group. In all experiments, the behaviour of the LFE individual was dramatically lower than that of the HFE individual. Individual LFE queens significantly reduced their rates of task performance in pairs for which they assumed this role compared to their own behaviour either as solitary individuals (Fig. 3) or within a prior pair in which they were the HFE (HFE–HFE pairs; Fig. 2). Additionally, when former LFE queens were paired, one of the two queens consistently increased her excavation activity relative to her prior association with an HFE (Fig. 2). This argues against fatigue as an alternative explanation for the other changes in task performance. These data support the assertion that division of labour is truly an emergent property with characteristics that extend beyond a simple summation of the component parts, and that the variation in behaviour that we measured was not simply a reflection of variance in the behaviour of individuals within the group.

If variance is central to task organization, what is the source of variation in the context of nest founding in *P. barbatus*? It may come indirectly from worker variation in excavation performance. The transfer of behavioural variation from a worker to a queen context would be consistent with our model. However, it is more likely that the variation occurs from selection on individual queens during nest formation. Colony mortality rates and the resulting selection pressures are vastly higher during this period than in any other period of the colony life-cycle. Foundresses face opposing pressures during this period from costs of desiccation from remaining on the surface without the protection of a nest, and from the numerous predators attracted to movement during excavation (Hölldobler, 1976b; J.H. Fewell, personal observation).

Emergent properties and selection on division of labour

Our results document that division of labour can emerge within simple social units, in the absence of selection. This is not to argue that selection has no role in the modification of task organization, or on the evolution of complex social units, such as seen in the eusocial Hymenoptera (Wilson, 1971; Hölldobler and Wilson, 1990). We simply argue that division of labour *originates* spontaneously within incipient social groups.

If so, it is not necessary to invoke selection to explain the origination or maintenance of task specialization in its basic form. Instead, we can ask the question of how selection acts on this basic structure to generate complex systems of task organization. One pathway

may be to increase the levels of intrinsic (genotypic) diversity in task performance among workers through multiple mating (polyandry) by the queen (Page and Robinson, 1991). Additionally, levels of specialization within a colony may be enhanced by an increase in genetic determination of task preference. In the complex environment of highly eusocial insect colonies, workers encounter numerous competing and potentially distracting stimuli. Genetically based task sensitivities can increase task efficiency by functioning as filters for the 'noise' produced by cues for other tasks.

In this study, we have documented specialization on a single task within a simple social unit. However, division of labour involves multiple individuals specializing on different tasks within a group. The variance-based model extends easily across multiple tasks. In the absence of strong genetic linkage for task preferences, we may expect that different members of a social group will vary in the task for which they are most sensitive, generating different specialists for different tasks. Additionally, individuals not specializing on one task are confronted with high stimulus levels for tasks not yet being performed, making it likely that non-specialists for one task by default specialize on other tasks in the nest.

Our experimental goal was limited to the demonstration that specialization on one task, in this case excavation, can emerge in social groups. However, it became clear that the non-excavating foundress was also performing a task. The LFE could generally be seen in the bottom of the chamber where the brood was located, while the HFE continued to excavate. Furthermore, all chambers with one or more queens became functional colonies with brood and/or workers, even though in most cases the excavator had died. Thus, our results suggest that the non-excavating foundress also specialized on a task: she became the reproductive specialist.

Variance-based division of labour across taxa

Our study generates the question of how universally the variance-based emergent property model can apply across social groups. We would expect from our model that sociality and division of labour are closely linked across a diversity of taxa. Sociality and division of labour have evolved independently multiple times within the Hymenoptera (Wilson, 1971; Michener, 1985), and occur across groups as diverse as termites (Wilson, 1971), aphids (Ito, 1989) and naked mole rats (Sherman *et al.*, 1991). We suggest that the inclusion of task specialization in the social structure of these groups is not a result of evolutionary convergence, but instead is an inescapable product of the variation that individuals bring to these groups.

Is there additional evidence that division of labour can be generated in incipient or artificially induced social groups? P.F. Kukuk (unpublished data) found strong asymmetry in performance of excavation tasks in the communal ground-nesting halictine bee, *Lasioglossum hemichalceum*. In observation colonies of unrelated, laboratory-reared females, some females spent a disproportionate amount of time digging at the end of the tunnel, while others moved loose soil to the nest entrance. Because the communal behaviour of *L. hemichalceum* occurs in a natural context, we cannot separate it conclusively from a history of selection. However, Sakagami and Maeta (1987) were able to generate forced associations of the solitary carpenter bee *Ceratina flavipes*. From a starting set of 178 females, they 'coerced' five pairs to nest together. In all five cases, one female became the primary egg layer and guarded the entrance while the other became the forager. Their results support the argument that task specialization can be generated as an emergent

property and further suggest that the emergent property model can be extended to the evolution of worker sterility.

Szathmary and Maynard Smith (1995) proposed eight major transitions to explain the apparent evolutionary increase in biological complexity from replicating molecules of proto-life to human societies. One of these transitions is from solitary organisms to cooperative groups. They considered the prime facilitator of this transition to be the development of division of labour, where individuals specialize on different tasks. Our results suggest that division of labour itself does not represent a separate evolutionary event, but instead may necessarily occur across social groups composed of intrinsically diverse individuals.

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