Dividing labour in social microorganisms: coordinated or random specialisation?

Guy Alexander Cooper*[1,2], Jorge Peña[3], Ming Liu[2], and Stuart Andrew West[2].

[1]St. John's College, Oxford, OX1 3JP, United Kingdom

[2]Department of Zoology, University of Oxford, Oxford, OX1 3SZ, United Kingdom

[3]Institute for Advanced Study in Toulouse, University of Toulouse Capitole, Toulouse, 31015 Cedex 6, France

Abstract

Division of labour, where cooperating individuals specialise to perform complementary tasks, plays a fundamental role at all levels of biological complexity, from genes to complex animal societies. Different labour-dividing species employ different mechanisms to determine how tasks are allocated between individuals, including coordinated, random, and genetic determination of phenotype (caste). It is not clear if this diversity is adaptive—arising because different mechanisms are favoured in different environments—or is merely the result of non-adaptive, historical artifacts of evolution. We analyse theoretically the relative advantages of the two dominant mechanisms employed for reproductive division of labour in social microogranisms: coordinated and random specialisation. We show that coordinated specialisation is more likely to evolve over random specialisation when: (i) social groups are small; (ii) cooperation has a greater relative impact on fitness (i.e., it is more "essential"); and (iii) there is a low cost to coordination. We also show how a fully coordinated group of cells can evolve step-wise from less precise forms of

* Corresponding author: guy.cooper@zoo.ox.ac.uk

coordination. Our predictions are in broad qualitative agreement with empirical patterns across microorganism species that divide labour. More generally, our results show how evolutionary theory can help explain both why between-individual coordination evolves, and why there is mechanistic variation between species.

Key words: division of labour, random specialisation, phenotypic noise, cellular differentiation, coordination, signaling, social microbes, adaptation, evolutionary theory

Introduction

Different species use different mechanisms to divide labour, with specialised phenotypes (castes) arising either randomly, through between-individual coordination, or by genetic control (Figure 1). Examples of between-individual coordination include workers feeding royal jelly to larvae to produce honey bee queens (Figure 1A), and how a lack of nitrogen fixation by neighbours causes cells of the bacteria *Anabaena cylindrica* to differentiate into sterile nitrogen-fixing heterocysts (Figure 1B) [1–3]. In contrast, in some ant societies whether individuals develop into queens, major, or minor workers has been found to have a strong genetic component (Figure 1C) [4–7]. Finally, in some bacteria, cell phenotype is determined randomly [8–13]. For example, in *Salmonella enterica* co-infections, random biochemical fluctuations in the cytoplasm determine whether a cell will infect the gut tissue and trigger an inflammatory response that eliminates competitors (and itself) (Figure 1D) [14,15]. Across the tree of life some species employ one mechanism to divide labour whereas in other species mixed forms exist with a combination of coordinated, genetic, or random specialisation [4,6,16].

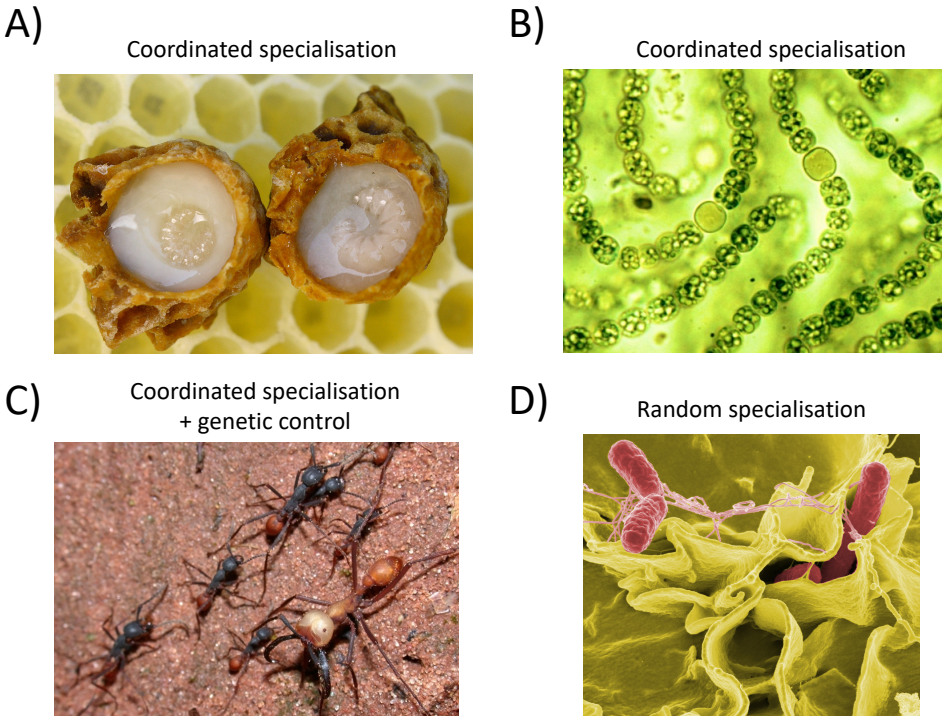

Figure 1. Different mechanisms for division of labour in nature. A) In honey bee hives (*Apis mellifera*), larvae develop as sterile workers unless they are fed large amounts of royal jelly by workers (coordinated specialisation) [1]. (Photo by Wausberg via the Wikimedia Commons.) B) In *A. cylindrica* filaments (cyanobacteria), some individuals develop into sterile nitrogen fixers (larger, round cells) if the amount of nitrogen fixed by their neighbours is insufficient (coordinated specialisation). This leads to a precise allocation of labour, with nitrogen-fixing cells distributed at fixed intervals along the filament [2]. (Picture taken by Robert Calentine.) C) In the army ant (*Eciton Burchelli*), whether individual ants become a major or minor worker has a genetic component (genetic control) [7]. (Photo by Alex Wild via the Wikimedia Commons, cropped.) D) In *S. enterica* infections (serovar *Typhymurium*), each cell amplifies intra-cellular noise to determine whether it will self-sacrifice and trigger an inflammatory response that eliminates competing strains (random specialisation). [15] (Photo by Rocky Mountain Laboratories, NIAID, NIH via Wikimedia Commons.)

We lack evolutionary explanations for why this diversity of labour-dividing mechanisms exists in the natural world [4,17–19]. Wahl analysed the relative advantage of genetic versus phenotypic control of division of labour, showing how genetic control can sometimes lead to groups in which not all complementary tasks are performed [18]. Wahl

focused on non-reproductive division of labour, such as that found between different worker castes within some social insect colonies. The other form of division of labour is that between helpers, who perform some costly cooperative behaviour, and pure reproductives, who do not perform the behavior [19–21]. It is this 'reproductive division of labour', common across the natural world from bacteria to insects, where the most variation in labour dividing mechanisms has been observed [19,20].

We focus our analysis on reproductive division of labour in social microbes, where two different mechanisms have been found: coordinated and random specialisation (Figure 2). Our aim is to examine whether the relative advantage of these two mechanisms can depend upon social or environmental conditions. Specifically, we use microbes as a 'test system' to determine whether evolutionary theory can explain diversity in the mechanisms underlying division of labour. We begin by assuming that coordinated specialisation leads to social groups containing the optimal allocation of helpers and reproductives. While this assumption is useful as a conceptual overview, such 'full coordination' may require a complex system of mechanisms and could be difficult to evolve from scratch. Consequently, in a secondary analysis we relax the assumption of full coordination and allow the level of coordination to co-evolve along with the extent to which labour is divided. This scenario is more biologically realistic and allows us to examine both whether coordination can initially arise and the extent of coordination favoured.

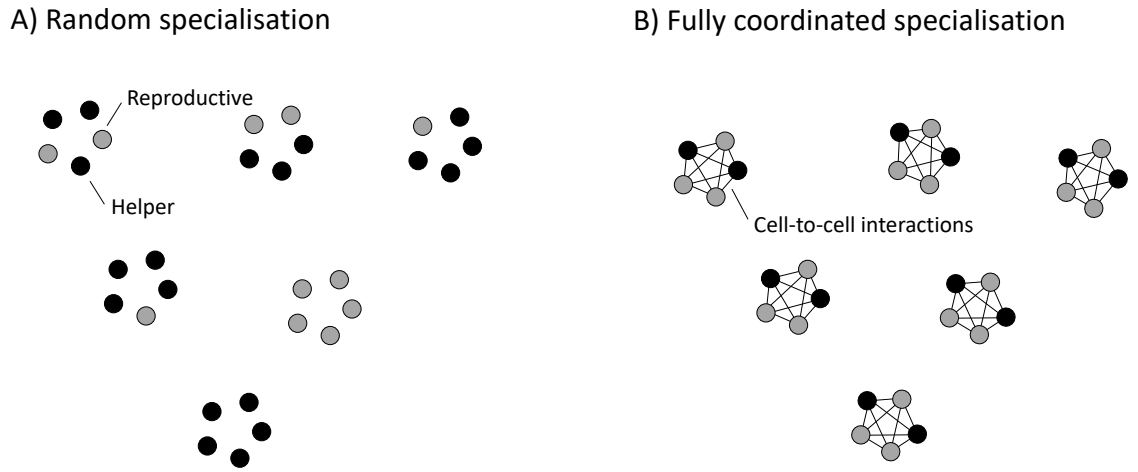

Figure 2. Mechanisms to divide labour in social microorganisms. We seek to determine the relative advantages and disadvantages of the two key mechanisms for reproductive division of labour in social microorganisms. (A) Random specialisation occurs when cells randomly specialise into helpers or reproductives independently of one another. This can occur when a genetic feedback circuit is used to amplify small molecular fluctuations in the cytoplasm (phenotypic noise) [8–10,12,14,22]. While potentially cheaper as a mechanism, random specialisation can lead to groups that deviate significantly from the optimal proportion of helpers and reproductives. (B) Coordinated specialisation occurs when cells interact with one another, and so share (or gain) phenotypic information while they are differentiating. This can arise through the secretion and detection of extracellular molecules (signals or cues), via the intermediary of parental control (epigenetics) or through relative condition dependence (signals or cues) [19,23]. While this mechanism can be metabolically costly, it produces precise groups with the optimal proportion of helpers and reproductives.

Results and Discussion

Random specialisation vs fully coordinated specialisation

We assume that a single individual arrives on an empty patch and, through a fixed series of replications, spawns a clonal group of n individuals consisting of k sterile helpers and $n-k$ pure reproductives ($k \in \{0,1,2,\dots,n\}$). The reproductive success (fitness) of a particular group (that we denote by $g_{k,n}$), as measured by the per capita number of dispersing offspring at the end of the group life cycle is given by

$$g_{k,n} = \frac{1}{n}(n-k)f_{k,n}, \qquad (1)$$

where $n - k$ is the number of reproductives in the group, and $f_{k,n}$ is the fecundity of each reproductive, which we assume is increasing in k.

Expression (1) highlights the trade-off between the number of reproductives in the group ($n - k$), which is higher when there are fewer helpers (lower k), and the amount of help that those reproductives obtain ($f_{k,n}$), which is higher when there are more helpers (higher k). The balance of this trade-off often results in an optimal number of helpers, k^*, that is intermediate (i.e., $0 < k^* < n$).

In species that divide labour by coordination, we assume that group members share phenotypic information via signalling between cells, parental control, or some cue of relative condition (Figure 2B). Our model is deliberately agnostic to the details of how phenotypic information is shared so as to facilitate broad predictions across different systems. Coordination allows the outcome of individual specialisation to depend on the phenotypes of social group neighbours. In our first analysis, we make the simplifying assumption that individuals coordinate fully, so that groups always form with the optimal number of helpers, k^*. The disadvantage of coordinated specialisation is that the mechanism of coordination can incur metabolic costs (e.g., from the production of extracellular signalling molecules). We posit that the fitness of a group of coordinated specialisers is given by:

$$w_C = (1 - c_n) g_{k^*,n} \ , \qquad (2)$$

where $g_{k^*,n}$ is the fecundity of a group with the optimal number of helpers (i.e., $g_{k^*,n} = \max_k g_{k,n}$) and $0 \leq c_n \leq 1$ is a multiplicative cost of coordination that we assume is

increasing in group size, n. A number of different models have examined the particular mechanisms that could be used to coordinate division of labour in specific systems [24–27].

In species that divide labour by random specialisation, each individual in the group independently becomes a helper with a given probability and a reproductive otherwise (Figure 2A). Hence, the final number of helpers in the group is a random binomial variable. Assuming that the probability of adopting a helper role is equal to the optimal proportion of helpers ($p^* = k^*/n$), the expected fitness of a group of random specialisers is given by:

$$w_R = \sum_{k=0}^{n} \binom{n}{k} p^{*k} (1 - p^*)^{n-k} g_{k,n}. \quad (3)$$

The potential advantage of random specialisation is that there are no upfront metabolic costs from, for example, between cell signalling. The downside of random specialisation is that groups sometimes form with fewer or more helpers than is optimal (demographic stochasticity). Wahl has discussed an analogous but mechanistically different cost that arises when division of labour is determined genetically: groups may sometimes form that do not contain all of the genotypes required to produce all of the necessary phenotypes (castes) [18].

Before proceeding, we must specify how reproductive fecundity depends on the amount of help in the group. We focus here on one of the most common forms of cooperation in microbes, where individuals secrete factors that provide a benefit to the local population of cells (“public goods”) [28]. We assume that the amount of public good in the social group depends linearly on the number of helpers in the group and is “consumed” by all

group members equally [29,30]. An example of such a public good is found in *Bacilus subtilis* populations, where helper cells produce and secrete proteases that degrade proteins into smaller peptides, which are then re-absorbed as a nutrient source by all cells [13].

We consider the possibility that the importance of producing public goods may vary. Accordingly, the fecundity of a reproductive is modelled as the sum of a baseline reproduction $(1-\epsilon)$ and of benefits derived from the production of public goods by helpers (scaled by ϵ). The parameter ϵ, which we call the essentiality of cooperation, quantifies the degree to which reproductives are reliant on helpers in the group [21]. As ϵ varies from zero to one, the production of public goods goes from being completely unimportant to entirely essential. These assumptions lead to the following expression for the fecundity of a reproductive:

$$f_{k,n} = (1-\epsilon) + \epsilon\frac{k}{n}. \tag{4}$$

Substituting Equation 4 into Equations 1-3 and solving for the condition for fully coordinated specialisation to be favoured over random specialisation (i.e., $w_C > w_R$), gives the simplified expression (see supplementary section C):

$$c_n < \frac{2\epsilon-1}{n}, \tag{5}$$

where division of labour is favoured to evolve only when $\epsilon > 1/2$, which we will assume henceforth. Condition (5) gives three key predictions for how the metabolic cost of coordination (c_n), the size of the group (n), and the essentiality of cooperation (ϵ) affect which labour-dividing mechanism is optimal (Figure 3).

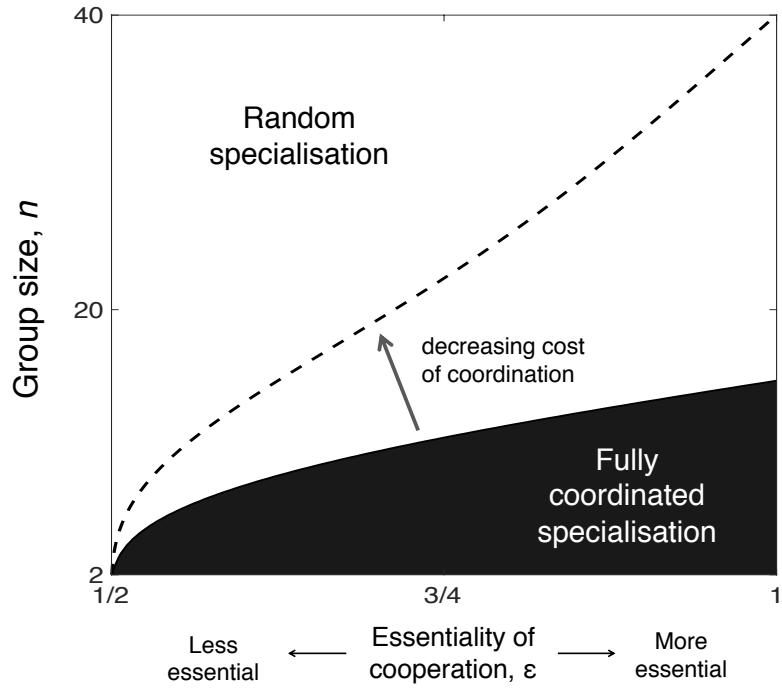

Figure 3. Random specialisation versus fully coordinated specialisation. We find that small group sizes (lower n), more essential cooperation (higher ϵ), and low costs to coordination (lower c_n) favour division of labour by fully coordinated specialisation (dark) over division of labour by random specialisation (white). We modelled the cost of coordination as the increasing and decelerating function $c_n = \alpha\left(1 - e^{-\beta n(n-1)/2}\right)$, where $n\,(n-1)/2$ is the number of cell-to-cell interactions in a coordinated group and $0 < \alpha < 1$ and $\beta > 0$ are parameters affecting the scale and the shape of the cost of coordination, respectively. Here, $\beta = 0.01$, and $\alpha = 0.1$ (solid boundary) or $\alpha = 0.025$ (dashed boundary).

If division of labour is favoured ($\epsilon > 1/2$) and there is no coordination cost for all n then coordinated specialisation is trivially always the preferred strategy (i.e., $w_C > w_R$ always holds). For positive coordination costs, condition (5) predicts:

Prediction 1: Smaller costs of coordination favour coordinated specialisation.

The relative costs of coordination will depend on the specific mechanism by which individuals ensure that the optimal allocation of labour is achieved. For example, signalling between social partners (as occurs in the formation of *Dictyostelium discoideum* fruiting bodies) could have higher costs than parental control (as occurs in Volvocine algae) or than using the products of cooperation as a cue (as occurs in *A. cylindrica)* [31–35].

If there is a cost to coordination, then the optimal mechanism to divide labour depends on how this cost balances against the hidden costs of random specialisation (i.e., the right hand side of inequality (5)). Theses hidden costs are determined by: (i) the likelihood that random groups deviate from the optimal proportion of helpers, and (ii) the degree to which those deviations from the optimal proportion of helpers leads to a reduced fecundity for the group (see supplementary section C). As captured by condition (5), the importance of these two factors depends upon the size of the group (n) and the essentiality of cooperation (ϵ).

Prediction 2. Smaller social groups favour coordinated specialisation.

Smaller groups favour coordinated specialisation for two reasons. First, the hidden costs of random specialisation are greater in smaller groups. In smaller groups, there are fewer possible outcomes for the proportion of helpers ($n + 1$ possible allocations of labour for groups of size n). Consequently, random specialisation can more easily lead to the formation of groups with a realized proportion of helpers that deviates significantly from the optimum ($p \ll p^*$ or $p \gg p^*$). In contrast, in larger groups there are more possible

outcomes and the resulting proportion of helpers will be more clustered about the optimal composition with highest fitness (with $p \approx p^*$ for very large group sizes).

This effect of group size on the cost of random specialisation is a consequence of the law of large numbers (e.g., one is much more likely have outcomes close to 50% heads when tossing 100 coins in a row compared to tossing 4 coins in a row, in which no heads or all heads may frequently occur). Our prediction here is also analogous to how, when mating occurs in small groups, small brood sizes select for less female biased sex ratios to decrease the probability of producing a group containing no males [36]. Similarly, in some cases random specialisation in a small group may strategically favour a lower (or higher) proportion of helpers than might otherwise be optimal, to decrease the chances of having zero or insufficient reproductives (or helpers; see supplementary section F and Figure S4).

The second reason why smaller groups favour coordinated specialisation is that in smaller groups there are fewer individuals with whom to coordinate and thus a smaller cost of coordination, given our assumption that c_n is increasing in n. The importance of this influence of group size depends upon mechanistic details about how specialisation is coordinated.

Prediction 3: More essential public goods favour coordinated specialisation

When cooperation is more essential (larger ϵ), the hidden costs of random specialisation increase, and so coordinated specialisation is more likely to be favoured. As the

235 essentiality of cooperation increases, the fitness costs incurred from producing too few
236 helpers also increases (i.e., there are larger costs to deviating from optimum). In addition,
237 as cooperation becomes more essential (larger ϵ), the fraction of helpers favoured
238 increases towards 50% helpers ($p^* \approx \frac{1}{2}$). This increases the variance in the proportion of
239 helpers, and so sub-optimal groups may arise more frequently (see supplementary
240 section C). Both of these effects increase the hidden costs of random specialisation, and
241 thus favour the evolution of fully coordinated specialisation (Figure 3).
242
243 Alternative forms of cooperation
244 The above analysis employs a deliberately simple public goods model, focusing on
245 factors that are expected to be broadly relevant across many microbial systems. This
246 facilitates the interpretation of our results, and generates broadly applicable predictions
247 that are less reliant on the specifics of any particular biological species.
248
249 In order to test the robustness of our results (predictions 1-3) we also developed a number
250 of alternate models for different biological scenarios (see supplementary sections D and
251 E, and Figures S1-S3). In particular, we examined the possibility that the collective good
252 provided by helpers: (i) is not consumed by its beneficiaries, as may occur when self-
253 sacrificing *S. enterica* cells enter the gut to trigger an immune response that eliminates
254 competitors (i.e., a non-rivalrous or non-congestible collective good); or (ii) is only
255 consumed by the reproductives in the group, as may occur for the fixed nitrogen produced
256 by heterocyst cells in *A. cylindrica* filaments (i.e., a kind of excludible good) [14,37,38].
257 We also examined the possibility that the fecundity of reproductives depend non-linearly

258 on the proportion of helpers in the group. In all of these alternative biological scenarios,
259 we found qualitative agreement with the predictions of the linear public goods model.
260
261 That said, we made a number of assumptions that it would be useful to investigate
262 theoretically. We assumed that social groups are always clonal, such that natural
263 selection would act to maximise group fitness [39,40]. Relaxing this assumption of
264 clonality would both decrease the optimal level of cooperation and increase the potential
265 for conflict within groups, which could for example undermine the stability and honesty of
266 inter-cellular signalling, making coordination less likely to be favoured [21,32,41].
267 Analogously, increasing within-group conflict could favour a genetic predisposition to
268 adopting a reproductive role in addition to the coordinated or random mechanism that
269 already exists [4,6].
270
271 <u>The optimal level of coordination</u>
272 Finally, we relax our assumption that individuals coordinate fully, and allow for
273 intermediate forms of coordination (Figure 4A). This allows us to examine whether costly
274 coordination can evolve from an ancestral state where there is no coordination. We
275 assume that coordination is achieved by one-to-one interactions between specialising
276 cells whereby phenotypic information is shared. We let s be the level of coordination,
277 which is equal to the probability that any two cells interact with one another. Once again,
278 our model is agnostic to the specific mode of interaction (whether it be via an extracellular
279 signal, or the intermediary of parental control, or otherwise) so as to generate predictions
280 that are not anchored to the specifics of a particular system. Cells randomly take turns

specialising, and adopt a helper role if the proportion of helpers amongst the cells with which they interact falls below a critical threshold, t (see supplementary section G.1 for more details on this model). We assume that higher levels of coordination (higher s) entail a larger cost of coordination c_n. Overall, this leads to a trade-off between more costly and precise forms of coordination on the one hand (higher s) and cheaper and less precise forms of coordination on the other hand (lower s). At the two extremes of s, we have either individual random specialisation with no coordination ($s = 0$), or full coordination between all cells ($s = 1$) (Figure 4A).

We used individual based simulations to determine the optimal level of coordination, s^*, and target proportion of helpers, t^*, that co-evolve in different scenarios (see supplementary section G.1, Figure 4B-D and Figure S5). The evolutionary outcomes, $s^*$and t^*, are estimated by the average trait values that evolved across the entire population, in the last 3,000 generations of the simulation, and over 10 independent simulation repetitions. The results of our simulations are in broad qualitative agreement with our previous predictions: small groups (low n) and more essential cooperation (high ϵ) favour the evolution of coordinated specialisation ($s^* > 0$; Figure 4D). Additionally, we found that both intermediate forms of coordination ($0 < s^* < 1$) and fully coordinated specialisation ($s^* \approx 1$) can be favoured to evolve, the latter occurring when group size is particularly small and cooperation is particularly essential (lower n and higher ϵ; Figure 4D). We find the same qualitative results with a simple analytical model (see supplementary section G.3). As well as potentially explaining variation across systems,

these results also suggest that individual cells could be selected to conditionally adjust their level of coordination in response to factors such as changing group size.

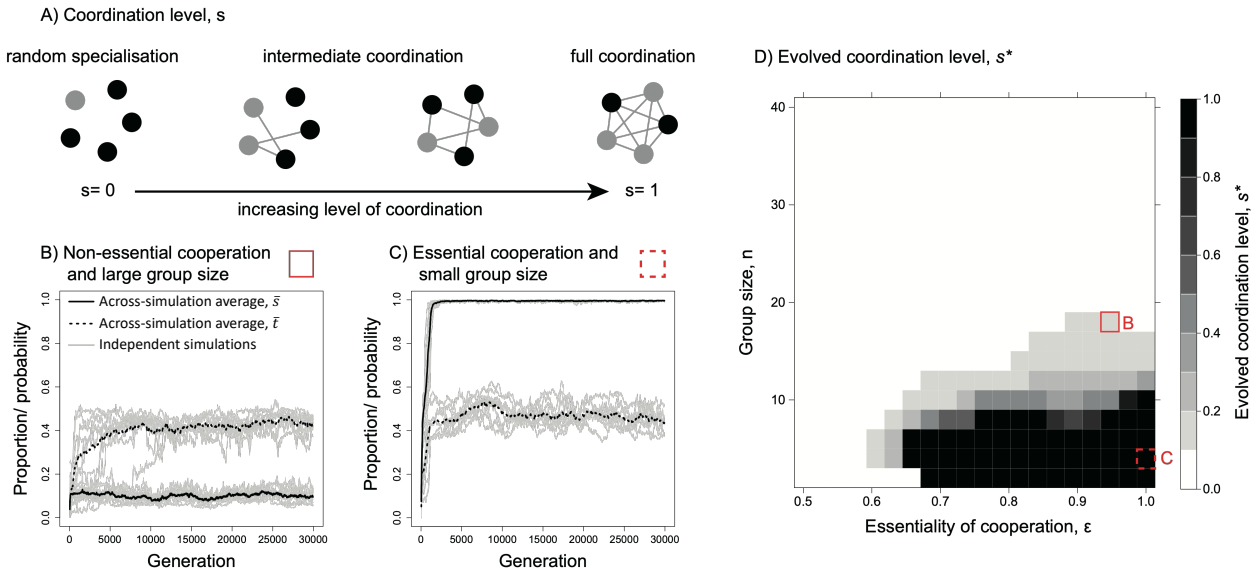

Figure 4. The optimal level of coordination. (A) If the level of coordination may evolve, then a spectrum of possible mechanisms could arise. At one extreme ($s = 0$), individuals may not coordinate at all (random specialisation). At the other extreme ($s = 1$), all individuals coordinate with one another and the variance in the realised proportion of helpers is minimised (fully coordinated specialisation). In between ($0 < s < 1$), intermediate forms of coordination may arise in which not all individuals coordinate with one another and sub-optimal proportions of helpers can occur. (B & C) We present the across-simulation average level of coordination ($\bar{s}$, solid line) and target proportion of helpers ($\bar{t}$, dashed line) over 30,000 simulation generations and where we have performed 10 independent simulation repetitions. We also plot individual simulation time series for the trait values (grey lines), where each line corresponds to a population average. We find that the traits converge stably within hundreds of generations. Moreover, the evolutionary outcomes (estimated by s^* and t^*, see supplementary section G.1 for more details), depend on demographic and environmental conditions: panel B corresponds to the middle red box in panel D, whereas panel C red box at the lower right corner. (D) Smaller groups (lower n) and more essential cooperation (higher ϵ) favour the evolution of fully coordinated specialisation ($s^* \approx 1$). Intermediate coordination ($0 < s^* < 1$) may evolve in more moderate conditions. (See figure S5 for the optimal target proportion of helpers, t^*). We modelled the cost of coordination as the increasing and decelerating function $c_n = \alpha\left(1 - e^{-\beta s n(n-1)/2}\right)$, where $sn\,(n-1)/2$ is the expected number of cell-to-cell interactions in a coordinated group with level of coordination s, and $0 < \alpha < 1$ and $\beta > 0$ are parameters that

affect the scale and the shape of the cost of coordination curve, respectively. Here, $\beta = 0.01$ and $\alpha = 0.1$.

Overall, these predictions highlight that the level of coordination within a labour-dividing species is a trait that can be shaped by natural selection, and that fully coordinated specialisation is a mechanism that can be expected to evolve via intermediate forms in many cases. We also found that the degree to which intermediate levels of coordination may arise depends on the shape of the costs of coordination (see supplementary section G.2 and Figure S6). In particular, if there is a large up-front cost to coordination, then intermediate coordination ($0 < s^* < 1$) is less likely to arise—random specialisation will either be favoured (no coordination; $s^* \approx 0$) or systems will tend to evolve to fully coordinated specialisation ($s^* \approx 1$). In microorganisms that divide labour by coordinated specialisation, both cyanobacterial filaments and *Volvox carteri* colonies have fully coordinated groups [42,43]. In contrast, the exact level of coordination in fruiting bodies such as *D. discoideum* and *Myxococcus xanthus* is less well known [44–46]. This highlights the need for further empirical work to determine the extent to which groups are "fully" coordinated in specific species.

<u>Distribution of labour dividing mechanisms in the natural world</u>

Most previous work on division of labour has tended to be either mechanistic, focusing on how different phenotypes are produced (caste determination), or evolutionary, focusing on why division of labour is favoured in the first place [1,4,17–21,24–26,33,34,47–53]. We have shown how evolutionary theory can also be used to explain why different mechanisms are used in different species [4,14,17–19]. In particular, we

have shown that coordinated specialisation is more likely to be favoured over random specialisation in small groups, when coordination costs are low, and when there are larger fitness costs to deviating from optimal caste ratios. Our results can help explain the distribution of mechanisms for division of labour that have been observed in bacteria and other microbes. Indeed, coordination appears to be more prevalent in species where group sizes are small, cooperation is more essential, and the cost of coordination is lower (Table 1; see also supplementary section H). However, this is speculative, as more data is required for a formal comparative study across species. Our results also suggest a hypothesis for why random caste determination has not been widely observed in animal societies: during the initial evolution of complex animal societies, group sizes were likely to be small and costs of coordination might have been minor compared to each individual's day-to-day organismal metabolic expenditure.

Species	Group size	Essentiality of cooperation	Cost of coordination	Type of specialisation
Salmonella enterica	Large	Low	High	Random
Bacilus subtilis	Medium	Medium	High	Random
Myxococcus xanthus	Large	Medium/High	Medium/High	Coordinated
Dictyostelium discoideum	Large	Medium/High	Medium	Coordinated
Volvox carteri	Large	High	Low	Coordinated
Anabaena cylindrica	Small	Medium/High	Low	Coordinated

Table 1: Division of labour in microbes. Examples of division of labour in bacteria and other microbes where the mechanism of specialisation has been identified [13–15,31,33,37,45,54,55]. For illustrative purposes, we provide approximate categorical estimates of relative group size, essentiality of cooperation, and the cost of coordination. This suggests roughly that coordinated specialisation has evolved most frequently in species with small groups, low coordination costs, and more essential cooperation. An across-species phylogeny-based comparative study, with a larger species sampling, would be required to formally test the predictions of our models [56]. This emphasizes the need for more data on the mechanisms underlying division of labour in these and other social microbe species (see supplementary section H). For example, persistence specialisation occurs randomly in large groups, and it has been suggested that this is cooperative [57].

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Data accessibility

All simulated data was generated using C and Matlab. The codes and generated data used for this study are available at:

https://github.com/mingpapilio/Codes_DOL_Mechanisms.

Author Contributions

G.A.C., S.A.W., and J.P. conceived the study. G.A.C. and J.P. and designed and analysed the analytical models, G.A.C. and M.L. designed and analysed the simulation models. G.A.C. and S.A.W. wrote the first draft. All authors contributed toward writing the final manuscript.

Declaration of Interests

The authors declare no competing interests.

403 ## Supplementary information:

404 **A. Overview**

405 **B. Labour dividers and their fitness**

406 **C. Linear public goods**

407 **D. Alternative modelling assumptions**

408 **E. Alternative forms of cooperation**

409 **F. Risk and insurance for random specialisers**

410 **G. The optimal level of coordination**

411 **H. Estimating the characteristics of social microbes**

412

413 **Figure S1. Alternative modelling assumptions**

414 **Figure S2. Non-linear public goods**

415 **Figure S3. Alternative biological scenarios**

416 **Figure S4. Risk and insurance for random specialisers**

417 **Figure S5. Optimal target proportion of helpers**

418 **Figure S6. The shape of the cost of coordination**

419

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