Division of labour and the evolution of extreme specialisation

Guy Alexander Cooper* and Stuart Andrew West
Department of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom

*Correspondence:
guy.cooper.ward@gmail.com

Abstract: Division of labour is a common feature of social groups, from biofilms to complex animal societies. However, we lack a theoretical framework that can explain why division of labour has evolved on certain branches of the tree of life but not others. We model the division of labour over a cooperative behaviour, considering both when it should evolve and the extent to which the different types should become specialised. We found that: (1) division of labour is usually—but not always—favoured by high efficiency benefits to specialisation and low within-group conflict; and (2) natural selection favours extreme specialisation, where some individuals are completely dependent upon the helping behaviour of others. We make a number of predictions, several of which are supported by the existing empirical data, from microbes and animals, while others suggest novel directions for empirical work. More generally, we show how division of labour can lead to mutual dependence between different individuals and hence drive major evolutionary transitions, such as those to multicellularity and eusociality.

Division of labour is a defining feature of complexity at all levels of biological organisation[1–5]. If individuals specialise to perform certain tasks, more complex social groups can evolve. In the extreme, if the different individuals become dependent upon the tasks performed by others, then a new ‘higher level’ individual may emerge. Examples include genes with different functions in a genome, cells that form distinct tissues in an animal, and castes that carry out different tasks in social insect societies. Consequently, in order to understand why complex life has evolved, we must understand the evolution of division of labour.

We lack theory that can explain why division of labour has evolved on some branches of the tree of life, but not others. Previous work has focused on clonal groups of cells and eusocial insects[6–14]. In both of these cases, it has often been assumed that the fitness interests of individuals are perfectly aligned, and so the evolution of division of labour is favoured if it increases group fitness (supplementary tables 1 & 2). However, division of labour also arises in species such as bacteria, slime moulds and cooperatively breeding animals where there can be appreciable conflict within groups and so cannot be assumed to be ‘superorganisms’[2,15,16]. If there is conflict within groups, then division of labour would not be selected for just because it increases group fitness[17–19]. Furthermore, if division of labour plays a role in driving transitions such as those to multicellularity and eusociality, then we need to understand how it can first evolve from individual level selection[2,4,20].

Division of labour can take different forms (Figure 1). In the simplest possible scenario, with only one cooperative behaviour, a division of labour consists of ‘helpers’ and ‘reproductives’ that may be specialized to varying degrees. The helper could be a fully specialised, sterile helper or a generalist that both helps and reproduces. Similarly, the more reproductive type could be a pure reproductive or a generalist that engages in some helping. This suggests four broad types of division of labour—from two different generalist types that help and reproduce at different rates, to the extreme case of a sterile helper paired with a pure reproductive (Figure 1). However, most models assume that only a certain type of division of labour is possible, often with fully specialised sterile helpers[7,9,10,12,18] (supplementary tables 1 & 2). Therefore, these models cannot be used to explain variation in the form that division of labour takes.

We theoretically model how a number of factors could influence selection for division of labour and its various forms. We wish to find the conditions that would favour both the initial evolution of division of labour, and the evolution of extreme specialisation, with individuals losing the ability to reproduce independently. We are interested in insights that could be applied across a range of different biological systems. Consequently, we construct a deliberately simple approximation, focusing on the trade-offs that we hypothesise are likely to be of general importance, rather than a complex model of a specific system[21].

Results

We consider an infinite population that is divided into social groups of fixed, finite sizes in which individuals engage in social interactions locally but offspring compete globally for niches in the next generation (island model). The genetic relatedness between individuals in a social group is given by R, which represents the relative probability that they are identical by descent (see methods).

We allow individuals to perform a costly cooperative behaviour, which increases the survival or reproductive viability of social group members. Specifically, a fraction $1 - \lambda$ of the benefit of cooperation goes to the focal individual and the remaining fraction λ is distributed to the other members of the social group (Figure 2c). We allow for potential efficiency benefits from greater cooperation with the parameter α (Figure 2b), which determines whether the benefits from increased cooperation are linear ($\alpha = 1$), accelerating ($\alpha > 1$) or decelerating ($\alpha < 1$). We vary the extent to which the cooperative trait is essential for survival with the parameter e. If $e = 1$, then cooperation is essential and individuals that reside in social groups with no cooperation have a fitness of zero. As e decreases, the trait is less essential and the cooperative behaviour becomes more of a luxury activity.

We allow for a division of labour into two phenotypes (Figure 2a). At the start of their life cycles, individuals terminally adopt phenotype 1 with probability p and phenotype 2 with probability $1-p$. Phenotype 1 invests a fraction q_1 of its lifetime efforts toward the cooperative trait and the remaining fraction $1 - q_1$ is allocated toward personal survival or reproduction. In contrast, phenotype 2 invests q_2 into the cooperative trait. When the two phenotypes differ, we will tend to assume that $q_1 > q_2$, such that, without loss of generality, phenotype 1 is more cooperative. Consequently, we are allowing three independent traits to co-evolve in our model: the level of cooperation of each phenotype (q_1, q_2), and the relative ratio of the two phenotypes (p). In our analysis, we used equilibrium theory to determine the strategy that is expected to evolve in the long-term (see methods and supplementary information 1, 2 & 3)[21,22]. The key predictions of our model are given in Table 1.

What types of division of labour are stable? Our model allows several possible strategies: uniform non-cooperation (no individuals help), uniform cooperation (all individuals are identical generalists that both help and reproduce) and four different types of division of labour (Figure 1). The types of division of labour are defined by the presence or absence of the extreme possible phenotypes: sterile helpers ($q_1 = 1$) and pure reproductives ($q_2 = 0$) (Figure 1). We found that uniform non-cooperation, uniform cooperation and division of labour could all arise as long-term evolutionary strategies (Figure 3).

We found that there was an evolutionary bias to more extreme forms of division of labour, where one of the phenotypes does all of the cooperation (Figure 3). The two types of division of labour that could be favoured were those with a pure reproductive ($q_2 = 0$) paired with either a generalist helper ($0 < q_1 < 1$) or with a sterile helper ($q_1 = 1$). In contrast, we did not find a region of parameter space where either of the other two types of division of labour, in which both phenotypes engage in cooperation, could evolve (Figure 3). Specifically, the combination of a generalist ($0 < q_2 < 1$) with either a more cooperative generalist ($q_2 < q_1 < 1$) or with a sterile helper ($q_1 = 1$) was never found to be stable. In supplementary information 4, we show that these results hold if we relax the assumption that cooperative costs are linear.

Why are intermediate forms of division of labour, where both phenotypes cooperate, not stable? We hypothesise that there may be an evolutionary feedback loop in which helper specialisation drives reproductives to help less and reproductive specialisation drives helpers to help more. In order to test this hypothesis, we developed dynamic, individual-based simulations as a proof of principle (Figure 4; supplementary information 5).

We held the level of cooperation in one phenotype fixed (q_1 or q_2) and allowed the other phenotype to evolve. We found that when phenotype 2 invested more resources into reproduction, phenotype 1 invested more resources into cooperation (lower q_2 drives higher q_1; Figure 4a). In turn, when phenotype 1 invested more resources into cooperation, phenotype 2 was driven more rapidly to pure reproduction ($q_2 = 0$; Figure 4b). More generally, the higher we fixed the level of cooperation of one phenotype, the higher the investment into reproduction of the other phenotype (Figure 4c).

To examine how these effects feedback on to each other, we considered the consequences of allowing just one phenotype to evolve for some time and before allowing both phenotypes to evolve. We initially held fixed the level of cooperation of phenotype 2 ($0 < q_2$ fixed), which lead to the other phenotype evolving to an intermediate level of cooperation ($q_1 < 1$; Figure 4d). When we then allowed both phenotypes to evolve, they always drove each other to the specialist extremes of pure reproduction ($q_2 = 0$) and sterile helping ($q_1 = 1$; Figure 4d).

The only intermediate form of division of labour that we find to be stable is the pairing of a generalist with a pure reproductive ($0 < q_1 < 1; q_2 = 0$). In a later section, we discuss how one of the conditions required for division of labour to be favoured is that there are efficiency benefits to specialisation ($\alpha > 1$). If division arises, we also found that the same condition ($\alpha > 1$) always favours the stability of pure reproduction ($q_2 = 0$). Consequently, whenever division of labour evolves, one phenotype will always be a pure reproductive ($q_2 = 0$). In contrast, efficiency benefits to specialisation ($\alpha > 1$) are necessary but *not* sufficient for the stability of a sterile helper ($q_1 = 1$). The evolution of a sterile helper therefore requires more restrictive conditions then a pure reproductive and thus an intermediate division of labour composed of the former phenotype but not the latter would never occur ($q_1 = 1; q_2 > 0$).

Division of labour in nature. Our prediction that more extreme forms of division of labour should be observed correspond to the patterns observed in the natural world. Considering cell groups, the most common form of division appears to be between sterile helpers and pure reproductives[15,23]. One of the clearest examples is the germ-soma divide in multicellular animals. Similarly, in microorganisms such as bacteria, fungi, algae and slime moulds, there are numerous examples of a sterile helper paired with a pure reproductive[18,24–27]. In contrast, less extreme division of labour involving a generalist paired with either a pure reproductive or a sterile helper appears to be relatively rare, with a single example of each from bacteria and algae respectively[28,29].

In animal groups, there appears to be two most common forms of division of labour. First, in the social insects, the divide between queens and their workers is between pure reproductive and sterile or effectively sterile-workers[2,3,7]. Second, in cooperative breeding vertebrates and invertebrates, the division is commonly associated with age—individuals help when young, and breed when old[2,16]. While our model captures the essence of why division of labour is favoured for these species, they also introduce a number of other factors, such as costs and benefits of cooperation varying with age, relatedness asymmetries, and individuals who are 'failed breeders'[16,30]. However, as predicted by our model, there are no known instances of division of labour in animals between a sterile helper and a generalist (that engages both in breeding and in helping others breed).

Our examination of the pattern in nature requires two points of clarification. First, in all these cases, the appropriate comparison is one trait at a time. So, pure reproductives with respect to one trait, may engage in other cooperative behaviours. For example, in the cyanobacterial division of labour, the cells that do not fix nitrogen are pure reproductives with respect to that trait, but can perform other cooperative traits, such as photosynthesis[24]. Second, there may be an observation bias towards discovering more extreme division of labour. Our prediction emphasizes the need for a quantitative survey of the types of division of labour in nature, rather than a reliance on just the systems that are being studied.

Our results do not categorically forbid the other two other types of division of labour in nature. Instead, our analysis offers a simple null model such that, if a form of division of labour not predicted by our model has evolved, then there must exist a complexity in the biological system not captured by our model and its assumptions. An example is provided by division of labour between sterile helpers and generalists in some Volvocine algae lineages[29]. When these algae reproduce, the reproductive cells must grow to the size of offspring colonies before reproduction. As such, any reproduction comes with a large commitment of resources, leading to helper sterility providing a large discontinuous resource bonus not contained in our model[6].

Relatedness and division of labour. A standard assumption has been that a higher relatedness favours division of labour[2,15,23]. Indeed, many models of division of labour have assumed the extreme relatedness of clonality, or that it is group fitness that is being maximised[6,7,9,10,12]. In contrast, we found that relatedness (R) has no influence on whether division of labour is favoured for essential traits ($e = 1$) that are required for reproduction or survival (Figure 3a-3b). A higher relatedness has no influence because the fitness benefit of being a pure reproductive is then exactly cancelled by the indirect fitness cost of not helping relatives in the group.

However, for non-essential traits ($e < 1$), a higher relatedness (higher R) does favour the evolution of division of labour (Figure 3c-3d). The main reason for this is that, as relatedness decreases, the indirect benefits of cooperation are reduced, and so uniform non-cooperation can outcompete cooperative division of labour[18]. Combining our trends, the overall prediction is that a higher relatedness (higher R) will favour division of labour for some traits (non-essential; $e < 1$), but not for other traits (essential; $e = 1$). The extent to which a trait is essential may change over evolutionary time—for example, a trait might start as relatively non-essential, and then become more essential as a group becomes more social, with more division of labour. In this case, relatedness could be more important for the initial evolution of division of labour than for its later maintenance. An empirical example is the subsequent loss of strict lifetime monogamy in some eusocial insects[31].

In the empirical data from multicellular groups, a higher relatedness is correlated with a greater likelihood of division of labour[23]. This is consistent with our model if the data are drawn only from non-essential traits, or a mix of essential and non-essential traits. In animal groups, a higher relatedness, due to lower levels of promiscuity, also leads to individuals being more likely to spend time as a helper in cooperative breeding vertebrates[32,33]. Our predictions suggest that it would be useful to further divide traits on the basis of how essential they are, and then test for how this interacts with relatedness.

Considering the different types of division of labour, our model predicts that a higher relatedness (higher R) favours more extreme division of labour regardless of whether the trait is essential or non-essential ($0 < e \leq 1$; Figure 3). In particular, a higher relatedness favours division between a sterile helper and pure reproductive ($q_1 = 1, q_2 = 0$) over division between a generalist and a pure reproductive ($0 < q_1 < 1, q_2 = 0$).

Our predicted influence of relatedness is consistent with the empirical data for multicellular groups, where groups with a higher relatedness are more likely to have sterile helpers[23]. Experimental evolution studies have also found that the sterile helpers are disfavoured at relatively low relatedness, in both slime moulds and fungi[34,35]. In animal groups, the division between sterile helper and pure reproductive also appears to be favoured by a higher relatedness, with eusociality having only evolved in sexual species that have strict lifetime monogamy, or asexual species that reproduce clonally[3,31,36].

In contrast to our predictions and the empirical data, some have argued that monogamy (higher R) may sometimes disfavour cooperation and division of labour[37,38]. However, subsequent work showed that these conclusions are based on restrictive assumptions. For example, in Nonacs's model, the best way for individuals to 'help' relatives is to disperse and reduce competition for resources rather than to stay and help kin[37,39]. In turn, the results of Olejarz et al.'s model are an artefact of constraining the analysis to the invasion of unconditionally expressed worker sterility in colonies where only an intermediate proportion of sterile workers is optimal (supplementary information 7.5)[38,40].

Clonal groups and lifetime monogamy. While higher relatedness tends to favour division of labour, our model shows that maximal relatedness ($R = 1$) is not required for division of labour to evolve, or even for the most extreme form of division between sterile helpers and pure reproductives ($q_1 = 1, q_2 = 0$; Figure 3)[18]. Many previous models of division of labour have assumed maximal relatnedness ($R = 1$), such that there is no conflict within-groups, and analysed how division of labour can maximise group fitness[6,7,9,11,12]. We have shown that division of labour can still be favoured, even with relatively low relatedness ($R < 1$) where there can be appreciable within-group conflict. This is consistent with Hamilton's rule, which showed how altruistic sterile helping can be favoured when $R < 1$[17,18]. More generally, this emphasises how division of labour can be favoured by kin selection at the level of the individual rather than simply by group efficiency maximisation.

Our prediction that maximal relatedness is not necessary is supported by cases where division of labour with sterile and reproductive helpers has been observed in non-clonal multicellular groups[23,26]. In social insects, lifetime monogamy leads to a potential helper being equally related to their siblings and their own offspring, which is equivalent to $R = 1$ in our asexual model[3,19,23,31]. Consequently, although eusociality has only evolved in species with lifetime monogamy or asexual reproduction, our theory shows that the initial evolution of division of labour, while favoured by maximal relatedness, does not require this condition in principle.

Ecological benefits and further predictions. Many previous models found that division of labour is favoured when there is an efficiency benefit to specialisation, with non-linear returns to increased cooperation ($\alpha > 1$)[6,11,12,41]. In supplementary information 7.1, we show that an efficiency benefit to specialisation ($\alpha > 1$) is necessary, but not sufficient for the evolution of division of labour (Figure 3)[9,42]. Instead our model also makes a suite of predictions for how the efficiency benefits of increased cooperation interact with a number of other factors (Table 1; supplementary information 7.2 & 7.3). For example, division of labour is more likely to evolve if the benefits of cooperation are generously shared between individuals (high λ), and if the trait is very essential for survival (high e).

Our model also makes predictions about the factors that favour the most extreme form of division of labour, with sterile helpers and pure reproductives (high α, λ, e and R), and the factors that determine the optimal ratio of helpers to reproductives, (p^*) (Table 1; supplementary information 7.4). These different factors can interact in unforeseen ways that qualitatively change predictions. For example, whether an increase in efficiency benefit of specialisation (α) and trait sociality (λ) leads to higher, lower or has no influence on the optimal proportion of helpers (p^*) can depend on the type of division of labour that is favoured (Figure 5).

Life-history and population demography. As we are interested in patterns that hold across a range of different biological systems, we constructed a deliberately simple model, focusing on the factors that we believe are likely to be of broad importance (see methods). For example, we purposefully left relatedness as an independent parameter ('open' model), and assumed that competition for breeding spots was global[21]. In some cases, for specific species, or groups of species, the way that the demographic processes generate relatedness patterns may be important for the evolution of division of labour. For these cases, our predictions may not hold and it could be useful to develop 'closed' models to examine how relatedness is determined by population demography and to make more targeted predictions[43]. We solve a closed model in supplementary information 6 and show that limited dispersal and overlapping generations both lead to higher relatedness in a way that favours the evolution of sterile helper and pure reproductive division of labour over uniform non-cooperation.

Broadly, our conceptual understanding of division of labour has been anchored to a limited number of complex systems, particularly the eusocial insects, cooperative breeders, and certain obligate multicellular organisms. Our model did not incorporate a number of factors that have been argued to be important in these systems, such as haplodiploid genetics, partially overlapping generations and large group sizes[2,6,17,44–46]. Furthermore, we did not restrict our model to the extreme case of maximal group relatedness, with clonal groups formed from single cells (or family groups from lifetime monogamy). Instead, our results show that the evolution of division of labour does not require such specific life-history characteristics and can evolve in much simpler cases. More generally, there is a rich precedent in evolutionary theory of using the predictions of simple models to better understand the behaviour of complex systems[2,21,22].

Conclusion

To conclude, we found that when division of labour is favoured, it tends to adopt extreme forms, involving pure reproductives that are dependent upon the helping behaviour of others. We found that helper sterility may evolve even with appreciable within-group conflict. This illustrates that division of labour is not merely a group level adaptation that evolves to maximise group efficiency[19]. Division of labour can be favoured by kin selection at the level of the individual and play a significant role in members of social groups becoming dependent upon each other. Consequently, division of labour is a driver, not a consequence, of major evolutionary transitions to higher levels of individuality, such as multicellularity and eusociality.

Methods

The fitness equation. We write the fitness of an individual as its expected fitness averaged across the possible phenotypes. Specifically, the neighbour-modulated (direct) fitness of a focal mutant with strategy (p, q_1, q_2) is given by:

$$\begin{aligned} W = p(1-q_1)\Big[(1-e) + e\big((1-\lambda)q_1^\alpha + \lambda(PQ_1^\alpha + (1-P)Q_2^\alpha)\big)\Big] \\ + (1-p)(1-q_2)\Big[(1-e) + e\big((1-\lambda)q_2^\alpha + \lambda(PQ_1^\alpha + (1-P)Q_2^\alpha)\big)\Big], \end{aligned}$$

where P, Q_1 and Q_2 are the average, others-only trait-values of social group neighbours[21,48,49]. The two terms (top row, bottom row) represent the realised fitness when of phenotype 1 (with probability p) and phenotype 2 (with probability $1-p$), respectively. Alternatively, the fitness equation may be conceptualized as the fitness of a founding individual of a social group, expressed as an expectation over the fitness of its descendants in the last generation of the social group before dispersal (haystack model.) The essentiality of the trait, e, is defined as the fraction of the realised fitness benefit that arises from cooperation rather than the asocial environment. The fitness benefit from cooperation in turn is composed of the benefit from personal investment in cooperation $((1-\lambda)(\ldots))$ and the benefit that arises from the investment of social group neighbours $(\lambda(\ldots))$. The benefit due to cooperation of social group neighbours is equal to $\sum_{i=1}^{N}(p_i q_{1,i}^\alpha + (1-p_i)q_{2,i}^\alpha)/N$, where i is an index of social group members that does not include the focal individual. We approximate this as $(PQ_1^\alpha + (1-P)Q_2^\alpha)$, which holds under rare mutation and weak selection (arithmetic mean is approximately equal to the geometric mean in this case.)

Equilibrium analysis. We seek the Evolutionarily Stable Strategy (ESS), (p^*, q_1^*, q_2^*), which is the strategy that, when employed by all individuals in the population, is uninvadable by a rare mutant lineage with an alternate strategy[22]. In supplementary information 1, we use numerical methods to determine the equilibria of the model, except in a number of special cases where we are able to solve for the equilibria analytically. An equilibrium point is defined as a joint strategy (p, q_1, q_2) for which directional selection in each trait is zero. We employ the directional selection forms developed by Taylor and Frank and Brown and Taylor[48,49]. For example, directional selection in p is given as $W_p(p, q_1, q_2) = \frac{\partial W}{\partial p} + R\frac{\partial W}{\partial P}$, where the partial derivative are evaluated for a monomorphic population $(p = P, q_1 = Q_1, q_2 = Q_2)$ and R is the relatedness of interacting individuals. We employ an open model approach and assume that R is a fixed, independent parameter of the model. An equilibrium strategy is then an ESS if it is uninvadable such that rare mutants are always less fit than an arbitrary individual in the equilibrium population. In supplementary information 2, we confirm that the equilibria of our model are uninvadable, and hence ESSs, with an analytical uninvadability analysis, numerical verification and individual-based simulations. In supplementary information 3, we use the methodology of Brown and Taylor to show that all of the ESSs analysed are convergent stable, such that the population is expected to evolve toward the equilibrium in trait-space[49].

Model assumptions. The construction of our model and its analysis relies on a set of life history, demographic and evolutionary assumptions, each of which may limit the applicability of the model in specific cases, for specific species. For example, we assumed that the population is infinite, structured into groups of fixed size, that reproduction is asexual with non-overlapping generations and that mutations are rare and lead to weak differences in selection. We also assumed that all competition is global. Taken as a whole, this constructs a model for division of labour that is only exact for very simple forms of life and we do not claim that our model makes exact predictions for division of labour in all species. However, we contend that our predictions should also hold broadly in nature when averaged across the tree of life. This will be true so long as our assumptions have not removed or rendered rigid a factor that is consistently important for the evolution of division of labour.

In some cases, factors that we have not modelled may be subsumed into the analysis. For example, although our model does not explicitly model the role of group size (N) in the evolution of division of labour, such predictions may be generated if we assume a relationship between group size and the other factors in our model. For example, in the Volvocine algae, it has been argued that the efficiency benefit of specialisation (α) is an increasing function of group size such that $\alpha = \alpha(N)$ and $\alpha'(N) > 0$. In this case, assuming that cooperation is favoured, we recover the previously found result that increasing group size N favours division of labour[6]. Alternatively, if the benefits of cooperation are shared less equally in larger groups (lower λ), then larger groups would disfavour division of labour.

In supplementary tables 1 and 2, we summarize how our model compares and links to previous theoretical work on the evolution of division of labour.

Code availability. Custom code used to demonstrate the uninvadability of the equilibria and the feedback effect driving extreme specialisation are available at osf.io/w6tzk.

Data availability. Data that was generated in our equilibrium analysis is avaliable at osf.io/w6tzk.

References

[1] Maynard Smith, J. & Szathmary, E. *The major transitions in evolution* (Oxford University Press, 1997).

[2] Bourke, A. F. *Principles of social evolution* (OUP Oxford, 2011).

[3] Boomsma, J. J. Kin selection versus sexual selection: why the ends do not meet. *Current Biology* **17**, R673–R683 (2007).

[4] West, S. A., Fisher, R. M., Gardner, A. & Kiers, E. T. Major evolutionary transitions in individuality. *Proceedings of the National Academy of Sciences* **112**, 10112–10119 (2015).

[5] Queller, D. C. Relatedness and the fraternal major transitions. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **355**, 1647–1655 (2000).

[6] Michod, R. E., Viossat, Y., Solari, C. A., Hurand, M. & Nedelcu, A. M. Life-history evolution and the origin of multicellularity. *Journal of theoretical Biology* **239**, 257–272 (2006).

[7] Oster, G. F. & Wilson, E. O. *Caste and ecology in the social insects* (Princeton University Press, 1978).

[8] Wilson, E. O. The ergonomics of caste in the social insects. *The American Naturalist* **102**, 41–66 (1968).

[9] Willensdorfer, M. On the evolution of differentiated multicellularity. *Evolution* **63**, 306–323 (2009).

[10] Rossetti, V., Schirrmeister, B. E., Bernasconi, M. V. & Bagheri, H. C. The evolutionary path to terminal differentiation and division of labor in cyanobacteria. *Journal of Theoretical Biology* **262**, 23–34 (2010).

[11] Ispolatov, I., Ackermann, M. & Doebeli, M. Division of labour and the evolution of multicellularity. *Proceedings of the Royal Society of London B: Biological Sciences* rspb20111999 (2011).

[12] Solari, C. A., Kessler, J. O. & Goldstein, R. E. A general allometric and life-history model for cellular differentiation in the transition to multicellularity. *The American Naturalist* **181**, 369–380 (2013).

[13] Rueffler, C., Hermisson, J. & Wagner, G. P. Evolution of functional specialization and division of labor. *Proceedings of the National Academy of Sciences* **109**, E326–E335 (2012).

[14] Tannenbaum, E. When does division of labor lead to increased system output? *Journal of theoretical biology* **247**, 413–425 (2007).

[15] West, S. A. & Cooper, G. A. Division of labour in microorganisms: an evolutionary perspective. *Nature Reviews Microbiology* **14**, 716 (2016).

[16] Arnold, K. E., Owens, I. P. & Goldizen, A. W. Division of labour within cooperatively breeding groups. *Behaviour* **142**, 1577–1590 (2005).

[17] Hamilton, W. D. The genetical evolution of social behaviour. i and ii. *Journal of theoretical biology* **7**, 1–52 (1964).

[18] Ackermann, M. *et al.* Self-destructive cooperation mediated by phenotypic noise. *Nature* **454**, 987–990 (2008).

[19] Gardner, A. & Grafen, A. Capturing the superorganism: a formal theory of group adaptation. *Journal of evolutionary biology* **22**, 659–671 (2009).

[20] Michod, R. E. Evolution of the individual. *The American Naturalist* **150**, S5–s21 (1997).

[21] Frank, S. A. *Foundations of social evolution* (Princeton University Press, 1998).

[22] Parker, G. A., Smith, J. M. *et al.* Optimality theory in evolutionary biology. *Nature* **348**, 27–33 (1990).

[23] Fisher, R. M., Cornwallis, C. K. & West, S. A. Group formation, relatedness, and the evolution of multicellularity. *Current Biology* **23**, 1120–1125 (2013).

[24] Flores, E. & Herrero, A. Compartmentalized function through cell differentiation in filamentous cyanobacteria. *Nature Reviews Microbiology* **8**, 39–50 (2010).

[25] Herron, M. D., Hackett, J. D., Aylward, F. O. & Michod, R. E. Triassic origin and early radiation of multicellular volvocine algae. *Proceedings of the National Academy of Sciences* **106**, 3254–3258 (2009).

[26] Strassmann, J. E., Zhu, Y. & Queller, D. C. Altruism and social cheating in the social amoeba dictyostelium discoideum. *Nature* **408**, 965–967 (2000).

[27] Velicer, G. J., Kroos, L. & Lenski, R. E. Developmental cheating in the social bacterium myxococcus xanthus. *Nature* **404**, 598–601 (2000).

[28] Veening, J.-W. *et al.* Transient heterogeneity in extracellular protease production by bacillus subtilis. *Molecular systems biology* **4**, 184 (2008).

[29] Herron, M. D. & Michod, R. E. Evolution of complexity in the volvocine algae: transitions in individuality through darwin's eye. *Evolution* **62**, 436–451 (2008).

[30] Koenig, W. D. & Dickinson, J. L. *Ecology and evolution of cooperative breeding in birds* (Cambridge University Press, 2004).

[31] Hughes, W. O., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320**, 1213–1216 (2008).

[32] Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969 (2010).

[33] Lukas, D. & Clutton-Brock, T. Cooperative breeding and monogamy in mammalian societies. *Proceedings of the Royal Society of London B: Biological Sciences* rspb20112468 (2012).

[34] Bastiaans, E., Debets, A. J. & Aanen, D. K. Experimental evolution reveals that high relatedness protects multicellular cooperation from cheaters. *Nature communications* **7** (2016).

[35] Kuzdzal-Fick, J. J., Fox, S. A., Strassmann, J. E. & Queller, D. C. High relatedness is necessary and sufficient to maintain multicellularity in dictyostelium. *Science* **334**, 1548–1551 (2011).

[36] Giron, D., Dunn, D. W., Hardy, I. C. & Strand, M. R. Aggression by polyembryonic wasp soldiers correlates with kinship but not resource competition. *Nature* **430**, 676 (2004).

[37] Nonacs, P. Monogamy and high relatedness do not preferentially favor the evolution of cooperation. *BMC Evolutionary Biology* **11**, 58 (2011).

[38] Olejarz, J. W., Allen, B., Veller, C. & Nowak, M. A. The evolution of non-reproductive workers in insect colonies with haplodiploid genetics. *Elife* **4**, e08918 (2015).

[39] Leggett, H. C., El Mouden, C., Wild, G. & West, S. Promiscuity and the evolution of cooperative breeding. *Proceedings of the Royal Society of London B: Biological Sciences* **279**, 1405–1411 (2012).

[40] Davies, N. G. & Gardner, A. Monogamy promotes worker sterility in insect societies. *bioRxiv* 059154 (2016).

[41] Michod, R. E. Evolution of individuality during the transition from unicellular to multicellular life. *Proceedings of the National Academy of Sciences* **104**, 8613–8618 (2007).

[42] Gavrilets, S. Rapid transition towards the division of labor via evolution of developmental plasticity. *PLoS Comput Biol* **6**, e1000805 (2010).

[43] Lehmann, L. & Rousset, F. How life history and demography promote or inhibit the evolution of helping behaviours. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **365**, 2599–2617 (2010).

[44] Seger, J. Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature* **301**, 59 (1983).

[45] Quiñones, A. E. & Pen, I. A unified model of hymenopteran preadaptations that trigger the evolutionary transition to eusociality. *Nature communications* **8**, 15920 (2017).

[46] Bonner, J. T. Perspective: the size-complexity rule. *Evolution* **58**, 1883–1890 (2004).

[47] Diard, M. *et al.* Stabilization of cooperative virulence by the expression of an avirulent phenotype. *Nature* **494**, 353–356 (2013).

[48] Taylor, P. D. & Frank, S. A. How to make a kin selection model. *Journal of Theoretical Biology* **180**, 27–37 (1996).

[49] Brown, S. P. & Taylor, P. D. Joint evolution of multiple social traits: a kin selection analysis. *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 415–422 (2010).

Acknowledgements

The authors would like to thank the following people for helpful discussion and comments on the manuscript: Sam Levin, Miguel dos Santos, Jay Biernaskie, Ashleigh Griffin, Charlie Cornwallis, Peter Taylor, Koos Boomsma, Daniel Unterwegger, Kevin Foster, Geoff Wild, Alan Grafen, Graham Taylor, Tobi Kiers and Roberta Fisher. We would like to acknowledge the use of the University of Oxford Advanced Research Computing (ARC) facility in carrying out this work. http://dx.doi.org/10.5281/zenodo.22558. G.A.C is funded by the EPSRC (EP/F500394/1).

Author contributions

G.A.C carried out the modelling work; G.A.C. and S.A.W. conceived the study and wrote the paper. All authors gave final approval for publication.

Competing interests

The authors declare no competing interests

Figure Legends

Figure 1: the different possible forms of division of labour. There are four broad forms of division of labour, each defined by the presence or absence of the two fully specialised phenotypes: pure reproductives (i.e. germline cells or social insect queens) and sterile helpers (i.e. somatic cells or worker castes). A *sterile helper and pure reproductive* division of labour (top left) is composed of both fully specialised phenotypes. The three other kinds of division of labour contain at least one generalist phenotype that invests in both tasks. In the strategy containing two different generalist phenotypes (bottom right), one of these phenotypes is cooperating at a higher level than the other.

Figure 2: a division of labour model. We consider a cooperative trait that individuals may invest in at a private cost. (a) The evolving traits. At the start of its life-cycle, an undifferentiated individual (top, shaded) stochastically adopts one of two phenotypes (middle). Individuals become phenotype 1 with probability p and phenotype 2 otherwise. Each phenotype invests a fixed amount of lifetime effort (q_1 or q_2) into the cooperative trait (bottom). When the two phenotypes differ, we tend to assume that phenotype 1 invests more into cooperation ($q_1 > q_2$). The traits p, q_1 and q_2 are the characteristics that are allowed to evolve in the model. (b) The benefits of cooperation. We allow for accelerating ($\alpha > 1$) or diminishing ($\alpha < 1$) returns to increased investment in cooperation. Each individual has a baseline benefit $1 - e$ regardless of the social environment. If $e = 1$, the trait is essential. Otherwise ($e < 1$), it is non-essential. The maximal return that can be attained via cooperation is then given by e (trait essentiality). (c) The trait sociality. A proportion λ of the returns from personal investment in cooperation will benefit social group neighbours equally (others-only; focal helper excluded.) The remaining $1 - \lambda$ benefits the focal helper alone. An additional parameter, R (not shown), quantifies the degree of relatedness within social groups of the population (others-only).

Figure 3: the evolution of division of labour. We examine how the various factors influence the strategy that is expected to evolve. Intermediate division of labour composed of generalists and pure reproductives is broadly favoured by increasing benefits to specialisation, high trait sociality, high trait essentiality and high relatedness. If these factors are pushed to further extremes, then an extreme form of division of labour with sterile helpers and pure reproductives may be favoured. No other form of division of labour is observed to be stable. See supplementary information 1-3 for more details.

Figure 4: the evolution of extreme specialisation. We hypothesized that there exists an evolutionary feedback loop whereby helper specialisation drives reproductives to specialise further on reproduction and reproductive specialisation drives helpers to help more. As a proof of principle, we tested this hypothesis with dynamic, individual-based simulations. (a) We find that the level of cooperation of the helper phenotype, q_1, evolves to higher levels of cooperation when the reproductive phenotype, q_2, is more fully specialised (low q_2; dashed) than when it is less specialised (high q_2; solid). (b) We find that the level of cooperation of the reproductive phenotype, q_2, evolves more quickly to pure reproduction ($q_2 = 0$) when the helper phenotype, q_1, is more fully specialised (high q_1; dashed) than when it is less specialised (low q_1; solid). (c) If we hold one phenotype fixed we find that the lower the level of cooperation of the fixed phenotype, the higher the level of cooperation of the evolving phenotype and vice versa. (d) If we hold reproductive specialisation (q_2) fixed for $10,000$ generations, then the level of helper cooperation (q_1) evolves stably to an intermediate value. If we then allow the level of cooperation of both phenotypes (q_1 and q_2) to evolve for another $10,000$ generations, then both phenotypes are driven to their specialised extremes ($q_1 = 1$ and $q_2 = 0$.) All error bars are 95 percent confidence intervals over simulation repetitions. See supplementary information 5 for more details.

Figure 5: the proportion of helpers and the level of cooperation. Our model makes a number of predictions about what form division of labour should take, including the optimal proportion of helpers and their level of cooperation. We found that the way certain factors affect the proportion of helpers depends on the form of division of labour that is favoured. For example, (a) if the helpers are

sterile ($q_1^* = 1$), then an increase in the efficiency benefits of specialisation (higher α) has no effect upon the optimal proportion (p^*) of helpers ($q_1^* = 1$). However, if the helpers are generalists ($0 < q_1^* < 1$), then a higher α decreases the optimal proportion of helpers (lower p^*). Similarly, (b) if the helpers are sterile ($q_1^* = 1$), then an increase in the sociality of the trait (higher λ) increases the optimal proportion (higher p^*) of helpers ($q_1^* = 1$). However, if the helpers are generalists ($0 < q_1^* < 1$), then a higher λ decreases the optimal proportion of helpers (lower p^*). These different predictions arise because, when there are generalists, the amount that they help (q_1^*) also changes (c and d). So for example, with a high efficiency benefit (higher α), we predict few generalists (lower p^*; a) but who help a lot (high q_1^*; c). In contrast, an increase in social group relatedness (higher R) or trait essentiality (higher e) leads to an increase in the optimal helper proportion (higher p^*) regardless of the form of division that is favoured ($0 < q_1^* \leq 1$; not shown). See supplementary information 7.4 for more details.

	Model Predictions	Empirical Validation?
When is division of labour favoured?	**1.** (a) If the trait is non-essential ($e < 1$), higher relatedness (higher R) favours division of labour. (b) If the trait is essential ($e = 1$), there is no effect of the value of relatedness.	Clonal cell groups ($R = 1$) are more likely to have a division of labour[23]. In animal groups, lower levels of promiscuity (higher R), leads to individuals being more likely to spend time as a helper in cooperative breeding vertebrates[32,33]. In all cases, distinction between essential and non-essential traits is not tested.
	2. (a) If relatedness, trait sociality and trait essentiality are high (higher R, λ and e), a higher efficiency benefit to specialisation (higher α) favours division of labour. (b) Otherwise, uniform non-cooperation may be favoured.	Formal test needed. However, greater group size does correlate with division of labour in some systems and this may be due to altered efficiency benefits[6,25,29].
	3. Higher trait sociality (higher λ) favours division of labour.	-
	4. If relatedness and trait sociality are low and the efficiency benefits are high (low R and λ; high α), a higher trait essentiality (higher e) favours division of labour.	-
	5. Depending on how group size (N) influences factors such as the efficiency benefits to specialisation (α), the extent to which the benefits of cooperation are shared (λ) or social group relatedness (R), a larger group may favour or disfavour division of labour.	Larger colony sizes have been found to favour division of labour in the Volvocine algae[6].
	5. The only forms of division that are favoured are those with a pure reproductive ($q_2 = 0$) paired with either a sterile helper ($q_1 = 1$) or a helper-reproductive ($0 < q_1 < 1$).	Formal test needed. Of the 7 discussed examples of microbial division of labour, 5 are sterile helper and pure reproductive, 1 is generalist and pure reproductive and 1 is sterile helper and generalist division of labour[24–29,47].
What kind of division is favoured?	**6.** Higher relatedness (higher R) favours helper sterility.	Clonal cell groups ($R = 1$) are more likely to have sterile cells[23]. Sterile helpers are disfavoured at low relatedness in both slime moulds and fungi[34,35]. In animal groups, eusociality has only evolved under conditions of strict lifetime monogamy (higher R)[3,31,36].
When are sterile helpers favoured?	**7.** (a) If relatedness, trait essentiality and trait sociality are high (high R, e and λ), higher efficiency benefits to specialisation (higher α) favours helper sterility. (b) Otherwise, higher efficiency benefits (higher α) may favour uniform non-cooperation.	-
	8. Higher trait sociality (higher λ) favours helper sterility.	-
	9. If relatedness and trait sociality are low and the efficiency benefits are high (low R and λ; high α), higher trait essentiality (higher e) favours helper sterility.	-
What affects the proportion of helpers?	**10.** Higher relatedness (higher R) favours a higher proportion of helpers (higher p^*).	Clonal cell groups ($R = 1$) have a higher proportion of helpers but study lacks phylogenetically independent comparisons and so is not statistically significant (more data needed)[23].
	11. (a) If the helpers are sterile ($q_1 = 1$), a higher efficiency benefits to specialisation (higher α) favours a lower proportion of helpers (lower p^*). (b) Otherwise, there is no effect.	-
	12. (a) If helpers are sterile ($q_1 = 1$), higher trait sociality (higher λ) favours a higher proportion of helpers (higher p^*) (b) Otherwise, higher trait sociality (higher λ) favours a lower proportion of helpers (lower p^*).	-
	13. Higher trait essentiality (higher e) favours a higher proportion of helpers (higher p^*).	-

Table 1: **Model predictions and empirical validation: the evolution of division of labour.** We present the key predictions of our model with respect to the conditions in which division of labour is favoured, what kind of division may be favoured, whether the extreme form of division with sterile helpers and pure reproductives is favoured and the factors that affect the proportion of helpers (if division is favoured.) We also specify whether the predictions have been previously tested empirically. The entry '-' implies that an empirical test is needed.