

Collective Action in the Fraternal Transitions

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Abstract

This paper examines an emerging paradigm that views higher-level evolutionary individuals as the products of kin selection. I name this the *SQB programme* after its foremost exponents, J. E. Strassmann, D. C. Queller and A. F. G. Bourke. In the first section, I outline the conceptual and methodological issues the SQB programme raises. In the rest of the paper, I subject the programme to more detailed scrutiny. I first consider the qualitative respects in which the social complexity characteristic of a highly integrated collective differs from cooperation conceived as a fitness transaction between individuals. These aspects of social complexity, while not incompatible with the SQB programme, are a potential source of novel explanatory challenges. I then home in on one feature in particular: the *extreme redundancy* exhibited by complex societies. I argue that extreme redundancy poses a distinctive explanatory puzzle for the SQB programme, and I offer a potential solution which casts kin-selected coercion as the crucial enabler. I suggest that the general moral to draw from the case is one of qualified optimism: while kin selection theory is a powerful tool for understanding transitions in individuality, it must be integrated within a broader framework that recognizes both the distinctive problems transitions present and the distinctive mechanisms by which these problems may be overcome.

1. Transitions in individuality as social phenomena

New work for kin selection theory

When we talk about *social behaviour* in the biological world, what exactly are we talking about? In a much-cited paper, Stuart West and colleagues (2007) compile a standardized lexicon for the study of social evolution. A social behaviour, they state, “has fitness consequences for both the individual that performs the behaviour (the actor) and another individual (the recipient)” (West et al. 2007, p. 418). The sign and magnitude of the fitness effects vary with the behaviour in question, giving rise to four subcategories: *mutual benefit* (+/+), *altruism* (□/+), *selfishness* (+/□) and *spite* (□□□□□□). The term “cooperation”, they suggest, should be reserved for behaviour “which provides a benefit to another individual (recipient), and which is selected for because of its beneficial effect on the recipient” (West et al. 2007, p. 419).

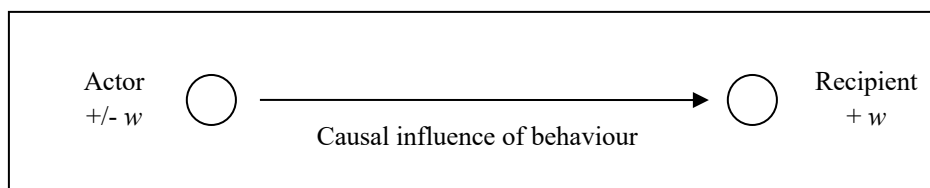


Figure 1. Cooperation as a pairwise fitness transaction.

Such a definition evokes a traditional and familiar picture of cooperation¹, a picture in which cooperation is understood on the model of a *fitness transaction* between two individuals, an actor and a recipient (Figure 1). Within this picture, the explanatory challenge

¹ Though the West et al. definition makes minor improvements, near-identical definitions can be found in, for instance, Hamilton 1964, Trivers 1985, Bourke and Franks 1995, and Bourke 2011.

cooperation presents is that the agents appear to be faced with a *prisoner's dilemma*, in which there is a strong temptation to defect and receive the benefits of cooperation (b) without paying the cost (c):

	COOPERATE	DEFECT
COOPERATE	$b - c$	$-c$
DEFECT	b	0

Provided b and c are positive, DEFECT dominates the payoff matrix: it delivers a better payoff than COOPERATE regardless of which strategy one's social partner chooses.

In the last three decades, the prisoner's dilemma has become a ubiquitous entry-point to theorizing about the evolution of cooperation, and we now have a highly detailed understanding of the ways in which cooperation can evolve in this kind of game (see, e.g., Colman 1995, Dugatkin 1997, Doebeli and Hauert 2005, Nowak 2006a). Indeed, all mainstream theoretical approaches to the evolution of cooperation may be regarded as ways of modifying this payoff matrix to make it more conducive to cooperation (see Nowak 2006b, Taylor and Nowak 2007). Of these, perhaps the best known is the *kin selection* approach, in which we consider *indirect fitness effects* weighted by the relatedness (r) of the actor to the recipient:

	COOPERATE	DEFECT
COOPERATE	$(b - c)(1 + r)$	$rb - c$
DEFECT	$b - rc$	0

From this modified payoff matrix, we can read off W.D. Hamilton's (1964a,b) famous rule: cooperation is stable when $rb - c > 0$.

The kin selection dissolution of the dilemma has proved remarkably influential. So influential, in fact, that it is sometimes even suggested that, in light of Hamilton's rule, only cooperation among *unrelated* individuals still represents a serious puzzle for evolutionary theory (see, e.g., Colman 2006). Yet two recent developments have presented this timeworn framework with new explanatory challenges.

One is a major re-evaluation of the place of cooperation in the history of life. Cooperation, once thought to be confined to a relatively small number of animal taxa, is now widely considered a central component of the Darwinian worldview (see, e.g., Nowak 2006a, Michod and Herron 2006, Calcott 2008, Queller and Strassmann 2009). This shift can be traced to the recent upsurge of interest in the *major transitions* in evolution, triggered in large part by the pioneering work of John Maynard Smith and Eörs Szathmáry (1995). When, instead of taking the biological hierarchy for granted, we view the history of life as a series of episodes in which new, higher-level individuals evolved from collectives of lower level entities, we start to see apparently cooperative phenomena where we saw none before: we see cooperation among cells within multicellular organisms, among organelles within cells, among genes within a chromosome. As Andrew F. G. Bourke observes in his recent synthesis, *Principles of Social Evolution*:

Social evolution has grown outwards from the study of the beehive and the baboon troop to embrace the entire sweep of biological organization. It claims as its subject matter not just the evolution of social systems narrowly defined, but the

evolution of all forms of stable biological grouping, from genomes and eukaryotic unicells to multicellular organisms, animal societies, and interspecific mutualisms. (Bourke 2011, p. 7)

The second development goes hand in hand with the first: it is the thought that well known approaches to the evolution of cooperation—kin selection theory in particular—might turn out to explain a great deal more than they were originally intended to explain. We can again turn to Bourke for a very clear statement of this view:

Hamilton's inclusive fitness theory (kin selection theory) provides a general theory of social evolution powerful and versatile enough to serve as the conceptual foundation for understanding the major transitions in evolution. (Bourke 2011, p. 27)

In a series of recent papers, Joan E. Strassmann and David C. Queller defend a similar line (Strassmann and Queller 2007, 2010, Queller and Strassmann 2009). They, like Bourke, see higher-level individuality as an essentially social phenomenon, and see kin selection as the key to understanding transitions in individuality. Moreover, they suggest that the successes of kin selection theory in explaining the behaviour of social insects provide strong evidence for this claim:

[Multicellular] organisms are groupings of cells ... how did they combine and make the transition to the unity of purpose of a single organism? Social insect groups can give us special insight into this question. We will argue that social insect colonies are much like organisms, and we will show how their unity of

purpose can arise through kin selection. (Strassmann and Queller 2007, p. 8620)

I want to distil these developments into two key claims, the conjunction of which I will refer to as the Strassmann-Queller-Bourke (SQB) thesis:

- (I) We can usefully regard evolutionary transitions in individuality as extreme examples of the evolution of cooperation.
- (II) For at least some transitions (specifically, the transitions from unicellular to multicellular organisms and from simple to complex sociality in the social insects), kin selection theory contains all the explanatory resources we need.

The aim of this paper is to subject this thesis to scrutiny. Note that, in framing (II), I have restricted its scope to the evolution of multicellularity and eusociality; below, following Queller (1997), I refer to these jointly as the *fraternal transitions*. This restriction does not imply that kin selection is *irrelevant* in the context of other transitions: indeed, provided we understand “relatedness” loosely enough, kin selection may well prove a valuable tool in explaining, for instance, the transition from lone replicators to replicators in compartments (see Michod 1983, Frank 1994, Szathmary and Maynard Smith 1997). There are, however, two reasons to single out the evolution of multicellularity and eusociality as of special interest. First, they are the transitions about which we have by far the most evidence, with the result that hypotheses about their causes tend to be empirically constrained to a much greater degree than hypotheses about transitions buried deeper in evolutionary history (Bourke 2011). Second, they are the transitions with regard to which kin selection seems most obviously relevant, since they involve the transformation of groups of related individuals. They are therefore the transitions with respect to which the SQB thesis is most tenable. Since, as I will argue presently, its tenability is an open question even in these apparently favourable

contexts, it seems charitable to restrict the scope of claim (II) to these contexts in the first instance.

Questioning the SQB thesis

Claim (I) may seem mundane at a glance: it is, after all, more or less a truism that transitions in individuality require cooperation among the lower-level entities. There is, however, more to (I) than this. The claim is not merely that the *initial stages* of a transition are examples of social evolution, or that transitions are *in part* driven by social-evolutionary processes. The claim is that transitions in individuality are social phenomena *from start to finish*, because the functional integration of a higher-level individual is nothing more than an extreme form of cooperation among its lower-level constituents. While it sounds plausible enough to talk of the functional integration of a complex insect society as a form of extreme cooperation among individual insects, it sounds rather more controversial to talk of the integration of a *multicellular organism* as a form of extreme cooperation among *cells*.² This is a bold contention, and it raises deep questions of both a proximate and an ultimate nature.

On the proximate side, consider the picture of cooperation with which we began: that is, cooperation as a fitness transaction between two individuals (Figure 1). We might legitimately fear that, in regarding interactions between the parts of an organism as an extreme form of cooperation, we are stretching this ordinary notion of “cooperation” to breaking point. For it sounds like one thing to say that the functional integration of a higher-

² The notion of the organism as a “cell state”, famously expounded by Rudolf Virchow and Ernst Haeckel, was influential in mid-nineteenth century biology but fell out of favour in the twentieth. See Reynolds 2007 for an overview of its history.

level individual can be viewed as a social phenomenon in a very broad sense, but quite another to say that it boils down to pairwise fitness transactions of the sort biologists tend to have in mind when they model social behaviour. There are at least two reasons why we might doubt the applicability of this model in the context of a transition in individuality, and both apply as much to the evolution of eusociality as to the evolution of multicellularity.

First, we might question whether, in the final stages of a transition, the lower-level constituents retain sufficient individuality to occupy the roles of “actor” and “recipient”. When a collective is integrated to a high degree, can we still regard the constituents as bearers of fitness in their own right? (If not, how can they donate and receive fitness?) And do they still have internal control over their own actions? (If not, can they really be regarded as evolutionary agents?) In both multicellular organisms and eusocial colonies, the constituent cells and insects remain countable and well-bounded, and they retain a capacity for something like reproduction (cells divide mitotically, while, with the exception of some ant genera, even “sterile” worker insects retain the capacity to produce male offspring; see Ratnieks 1993), so they may be considered Darwinian individuals in a minimal sense (see Godfrey-Smith 2009, 2011). Yet they are incapable of surviving for long outside the larger unit, and they appear to have lost a great deal of the behavioural autonomy their ancestors once possessed. As a result, they seem very different from paradigm evolutionary agents. How important are these differences?

Second, even granting that the constituents of a higher-level individual may legitimately be viewed as engaged in a form of social interaction, we might question whether a two-party fitness transaction remains the appropriate model for these interactions. When cells or social insects exhibit cooperative behaviour, are the relevant interactions still between *pairs* of individuals? Are the fitness benefits gained by a recipient always attributable to a single behaviour by a specific actor? Can a determinate recipient be identified for every

cooperative action? If not, then a conception of transitions in individuality as extreme examples of the evolution of cooperation may entail radical revisions to our traditional conception of a cooperative interaction.

These proximate questions naturally lead to an ultimate question: if viewing transitions as extreme examples of the evolution of cooperation indeed requires that we acknowledge forms of cooperation qualitatively different from a pairwise fitness transaction, what are the implications for our understanding of how cooperation *evolves*? Will standard approaches designed to explain pairwise cooperation in the prisoner's dilemma carry across straightforwardly to a transitions context? Or will explaining the kinds of cooperation characteristic of a higher-level individual call for novel explanatory approaches?

Given the role assigned to it in claim (II), kin selection theory merits particular scrutiny in this regard. Claim (II), like claim (I), may look uncontroversial at a glance, for the constituents of multicellular organisms and eusocial colonies often exhibit high relatedness. The thought arises that this pattern can hardly be coincidental, and that it may provide a clue to the process by which these entities arose: relatedness was surely part of the story (Queller 2000). As with (I), however, the claim I want to consider is considerably stronger than this. The claim is not simply that kin selection is important in the *initial stages* of a fraternal transition, or that it is one factor among many that drives such transitions towards completion. The claim is that kin selection is instrumental at *every stage*, and that kin selection theory explains not merely how social groups *form* and *persist* but also how those groups are *transformed* into higher-level *individuals* (see Bourke 2011, Ch. 1). We might reasonably question whether kin selection theory can do all this alone. We might wonder in particular whether kin selection is still the driving force in the final stages of a transition, when stable groups of lower-level entities acquire the characteristic features of organismal complexity.

These are open questions. In the rest of the paper I explore them further, with a view to assessing the prospects for the research programme the SQB thesis embodies. In Section 2, I turn specifically to proximate matters: what are the distinctive features of highly integrated collectives, and how do they challenge our traditional conceptions of biological cooperation? In Section 3, I focus on the role of *extreme redundancy* (in a sense I will articulate) in transforming collectives from groups to individuals. I then argue that redundancy generates a problem for the SQB programme: when redundancy is extreme, agents face a form of social dilemma that an appeal to indirect fitness effects does not straightforwardly dissolve. I suggest how the challenge of explaining the evolution of extreme redundancy might nevertheless be met. In Section 4, I close by drawing some general morals for the SQB programme in light of these considerations.

2. Proximate aspects of social complexity

We began with a picture of cooperation as an interaction in which the behaviour of an actor causally influences the fitness of a recipient. We then considered the suggestion that evolutionary transitions in individuality may be usefully regarded as extreme examples of the evolution of cooperation. And we noted a tension between these ideas: if we are to view the functional integration of a higher-level individual as a form of cooperation among its constituents, we may have to expand our traditional picture of what cooperation involves. In this section, I survey some distinctive features of multicellular organisms and the most complex eusocial colonies. These are features that distinguish social *complexity* from mere sociality, and which any theoretical framework that professes to explain transitions in individuality needs to be able to account for.

Task-based cooperation

To better understand the nature of social complexity, we can turn to the proximate literature on eusociality. The work of Carl Anderson, Nigel R. Franks and Daniel W. McShea is particularly valuable in this context (see Anderson and McShea 2000, Anderson and Franks 2001, Anderson, Franks and McShea 2001). Anderson, Franks and McShea begin by observing that the most unmistakable feature of cooperation in eusocial societies—and the root of many further complexities—is that it takes the form not of isolated behaviours but of *collective tasks*, where a task is “an item of work that potentially [i.e., if completed] makes a positive contribution, however small, to inclusive fitness” (Anderson et al. 2001, 644).³ While some tasks may be completed by a single individual, many require multiple contributions. The general picture in such cases is not the familiar picture of a single actor conferring a benefit on a recipient: it is one of many actors collaborating to confer a benefit through task completion (Figure 2). The recipients may be the same individuals as the actors (as in the case of a task performed by a number of individuals for their mutual benefit) but they need not be; indeed, in the kinds of cases that will concern us here—cases in which the recipient is a queen or a germ cell—the recipients rarely participate in any tasks, and the actors rarely gain any personal fitness benefit from their own efforts.

³ The emphasis on *inclusive* fitness here is redundant. Since an item of work can only contribute to the inclusive fitness of an individual by contributing to the fitness of that individual or a relative, we might equally define a task as “an item of work that potentially makes a positive contribution to fitness”.

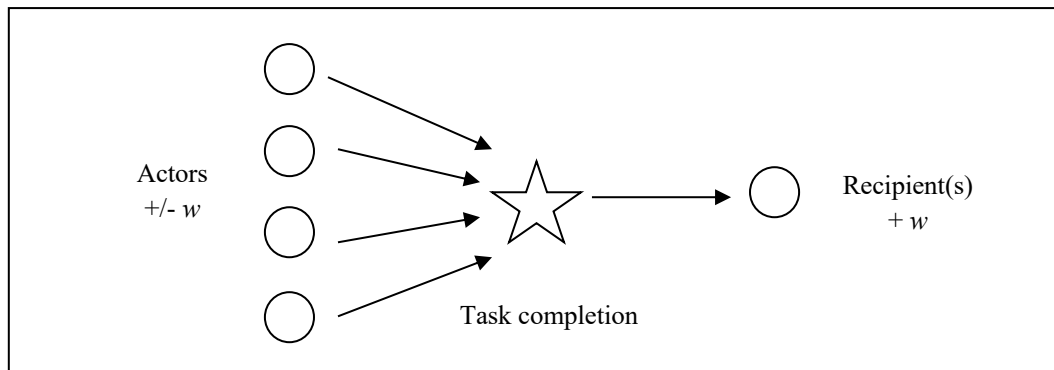


Figure 2. Task-based cooperation.

Note that, even on the highly idealized picture of task-based cooperation shown in Figure 2, it is unclear how, if at all, we can resolve the benefit conferred on the recipient into discrete components contributed by each of the actors. Should we say that each actor contributed B/n , where B is the total benefit conferred and n is the number of actors? Or should we say that each actor contributed $B - B^*$, where B^* is the reduced benefit that would have been conferred if that actor had not participated? The former measure takes no account of the fact that some actors may make a greater contribution to the task than others, while the latter measure allows that the total benefit conferred by the actors may differ from the total benefit received by the recipient.⁴ Neither, therefore, is satisfactory. But if the total benefit of task completion cannot be resolved into discrete individual contributions, the pairwise fitness transaction picture breaks down: task completion confers a benefit on the recipient that is not reducible to the sum of the benefits conferred by the individual actors considered separately (Figure 3).

⁴ Suppose, for instance, that every contribution is needed for the completion of the task, so that $B^* = 0$ and $B - B^* = B$. On this measure, the benefit conferred is nB , but the benefit received is only B .

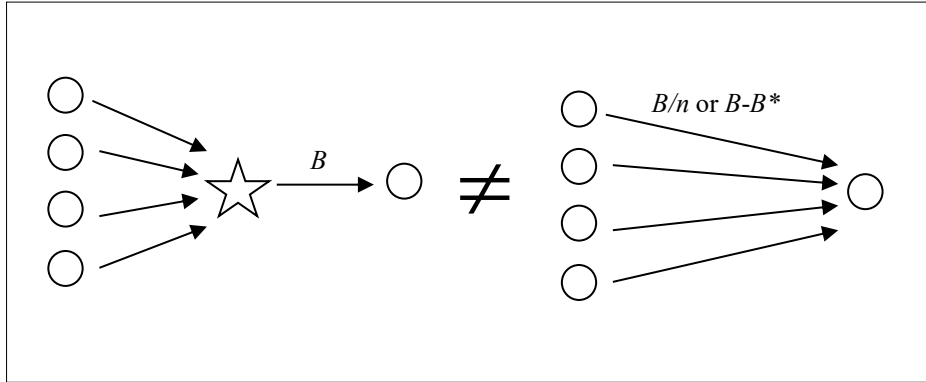


Figure 3. The benefit of task completion does not straightforwardly decompose into discrete, additive components.

Of course, the failure of these two simple measures hardly shows that the overall benefit *could not* be resolved into discrete components: some more complicated measure may yet succeed where the simple measures fail.⁵ But it does show that decomposing the benefit of task completion is by no means a straightforward business: even in very simple cases, we can see how acknowledging the task structure of cooperation puts the pairwise fitness transaction model under strain.

⁵ Here is one possibility: each actor contributes a share weighted by the relative difference their contribution makes to the total benefit. Formally, let b_i represent the benefit conferred by the i^{th} individual and let B_i^* represent the total benefit that would have been conferred had that individual unilaterally defected. The proposal is that:

$$b_i = \frac{B}{n} \cdot \frac{B - B_i^*}{\sum_i^n (B - B_i^*)}$$

This measure lacks the obvious defects of the simpler measures, but more work is needed to show that it provides a useful decomposition of the overall benefit for the purpose of understanding the relevant evolutionary dynamics. For instance, does Hamilton's rule still apply when benefit is calculated using this measure? I will not undertake this work here, since it is peripheral to the overall argument.

Further complications

I now want to introduce four further features that add to the complexity of task-based cooperation. While the features I will consider are by no means wholly absent from simpler forms of social group, complex societies tend to exhibit them to a much greater degree. The list is not intended to be exhaustive; moreover, since my primary aim is to relate these features to ultimate questions, I will describe each only briefly (see Anderson and McShea 2001 for a more detailed synthesis).

1. Division of labour

Informal talk of division of labour is widespread in discussions of the major transitions (see, e.g., Maynard-Smith and Szathmary 1995, Godfrey-Smith 2009, Bourke 2011), but Anderson, Franks and McShea deploy the notion in a relatively technical sense. For Anderson, Franks and McShea, labour is divided when a task is divided into more than one distinct *subtask*, where a subtask is an item of work that would not by itself confer a fitness benefit but that fulfils one of the necessary conditions for the completion of a larger task. Subtasks may themselves be divided into further subtasks, and so on. Anderson, Franks and McShea provide no algorithm for the individuation of subtasks, but suggest that in practice the subtasks are often easily identified (for instance, they describe a grass harvesting task in *Hodotermes mossambicus*, where the workforce is visibly divided into cutters and transporters (Anderson et al. 2001, p. 645)). By conceptualizing division of labour in this way, we make the notion distinct from that of *specialization* (see below). Indeed, they are properties of different things: *tasks* are divided, while *workers* are specialized. This conceptual distinction, though rarely drawn explicitly, is a helpful one, because the division of a task into subtasks may occur without the specialization of workers, and vice versa.

2. *Specialization*

Specialization is correlation between the properties of workers and the tasks they undertake.⁶ It thus requires some form of *differentiation* among workers. In the eusocial Hymenoptera, two kinds of specialization predominate: specialization based on *morphological* differences (in which workers undertake different tasks depending on their physical characteristics) and specialization based on *age* differences (in which workers typically perform different tasks at different life stages). As Anderson and McShea (2001) note, however, some cases of specialization fall in between these categories. These are cases in which workers develop traits that enable them to perform a particular task at a particular life stage, only to lose those traits subsequently (they cite the short-lived production of royal jelly in honey bees, which leads to the temporary specialization of workers in feeding tasks). Polymorphism and age-based polyethism can thus blur into one another: we can do better by seeing these as extremes of a continuum of specialization based on developmental differences, ranging from superficial, short-lived differences in the simplest colonies to spectacular, life-long polymorphism in the most complex.

I want to reserve the term *extreme* specialization for cases in which specialization is accompanied by a loss of behavioural totipotency—in other words, cases in which workers have lost the ability to undertake some or all tasks other than the task for which they are specialized. While eusocial societies with distinct morphological castes exhibit some degree of extreme specialization, multicellular organisms display this phenomenon to a far greater degree: consider, for example, a human red blood cell, which specializes so exclusively in

⁶ Because specialization may be regarded as a kind of correlation, we can quantify the overall degree of specialization in a social group using information theory (see Gorelick et al. 2004). It is thus perhaps the only aspect of social complexity for which a reasonably straightforward quantitative measure is available.

oxygen transport that it lacks even a nucleus—a basic prerequisite for participation in most other tasks.

Germ-soma specialization occurs when some group members specialize in tasks which contribute to the growth and persistence of the collective, while others specialize in tasks which generate new collectives. Germ-soma specialization may be extreme, such that somatic specialists lose the capacity to generate new collectives, but it need not be (in plants, for instance, all cells in the floral meristem can potentially give rise to new individuals; see Clarke 2011). Owing to its consequences for within-group conflict, germ-soma specialization is often assigned special importance in accounts of the major transitions (see, e.g., Buss 1987, Michod 2007, Godfrey-Smith 2009, Bourke 2011).

3. *Coordination*

Coordination is a feat of signalling and plasticity. It introduces yet more contingencies on which the success of a task may depend: when a task requires coordination, the subtasks must be performed at the right time and in the right order. As Anderson and Franks (2001) take pains to point out, while coordination presupposes a division of labour, it may not always require specialization: a task must be split into subtasks, but the workers who undertake the subtasks need not belong to different specialized castes.

Among coordinated tasks, Anderson and Franks distinguish *partitioned* tasks, in which the subtasks take place in a coordinated *series*, from *team* tasks, in which the coordinated subtasks occur *concurrently*. While partitioned tasks are fairly widespread in eusocial societies (particularly tasks which exhibit a “bucket brigade” style organization; see Ratnieks and Anderson 1999), team tasks appear to be relatively rare (Anderson and Franks cite nest construction in *Oecophylla* weaver ants, prey retrieval in *Eciton burchelli* and *Dorylus wilverthi* army ants, and the decapitation of intruders in *Pheidole pallidula* ants). This

is far from the case in multicellular organisms, where teamwork is rife: consider, for instance, a coordinated muscle contraction, or the coordinated production of enzymes.

4. Redundancy

A workforce contains *redundancy* when there are more workers than are strictly needed for task completion. We see two broad kinds of redundancy in insect societies. The first sort (which I will call *inactive redundancy*) occurs when there is a large *reserve workforce*, idle but ready to step in should any labour shortages arise. This phenomenon is widespread in eusocial societies (see Hölldobler and Wilson 1990, pp. 342-343). The second (which I will call *active redundancy*) occurs when more workers actively undertake a task than are strictly necessary for its completion. We see this in the foraging strategies of complex ant societies: large numbers of ants search for food in parallel, then work in parallel to retrieve the food that one individual has found (see Oster and Wilson 1978, Herbers 1981). The upshot of redundancy in either form is that “if one worker doesn’t complete the task someone else will” (Oster and Wilson 1978; see also Section 3). We see a clear analogue of this phenomenon in multicellular organisms, where the number of cells that specialize in a given task often dramatically exceeds the minimum required for task completion. To take a particularly extreme example, the human circulatory system can stand to lose one eighth of its total stock of red blood cells during a routine blood donation without any significant adverse effects.

Redundancy will receive further attention below. In the present context, I want to distinguish what I have called redundancy (following Anderson and McShea 2001, and Hölldobler and Wilson 1990) from a very different phenomenon to which the same name has been applied. Andrew F. G. Bourke and Nigel R. Franks (1995, p. 440) contrast what they term the *redundancy of parts* (that is, the existence of surplus workers, which I am calling simply *redundancy*) with what they term the *redundancy of functions*. By “redundancy of

functions”, they mean an individual worker’s latent capacity to undertake tasks that they are never called upon to perform during their lifetime. I will call this phenomenon *latent versatility*. The issue is terminological but important nonetheless, since the contrast between redundancy and latent versatility will play a key role in Section 3.

From proximate to ultimate

Even a very brief overview of the complexities of cooperation brings the limitations of the pairwise fitness transaction model to the fore. If we focus only on explaining pairwise cooperation in the prisoner’s dilemma, we will leave many of the most striking features of social complexity unexplained. This is not to say that traditional approaches to the evolution of cooperation are *irrelevant* in the context of the transitions. It is merely an acknowledgement that, when we switch to a transitions context, new explananda come into view. An adequate theory of evolutionary transitions in individuality needs to explain more than pairwise cooperation: it must also explain the complexities of task-based cooperation. It is an open question whether kin selection theory has the resources to meet that challenge. To get closer to an answer, I want to home in on one particular aspect of social complexity that has gone largely neglected in previous discussions of the major transitions.

3. Redundancy in focus

The roles of redundancy

In the opening pages of their seminal work, *Caste and Ecology in the Social Insects* (1978), George F. Oster and Edward O. Wilson identify redundancy (along with caste specialization and division of labour) as a fundamental feature of complex sociality (see Oster and Wilson 1978, pp. 11-15; see also Hölldobler and Wilson 1990, pp. 356-358). As Oster and Wilson emphasize, redundancy (or, in their terms, task structures based on parallel operations) is essential to the stability of a colony and instrumental in generating benefit for social over solitary living. The reason is that redundancy assures the *robustness* of task completion in the face of individual failure. When overall task success requires that *every* worker completes its subtask, the overall reliability (that is, the probability of task completion) can be no greater than the product of reliabilities of the individual workers. By contrast, when the task structure contains redundancy (whether active, inactive, or both), the overall reliability can vastly exceed this product. When duplicate roles are performed in parallel, or when reserves are ready to step in should individual workers fail, overall task completion may remain highly probable even given a reasonably severe rate of worker attrition.

Redundancy, then, generates benefit for group living by enhancing the robustness of task completion.⁷ But it may have an even more significant role to play in evolutionary transitions: the achievement of robustness through redundancy—rather than through latent versatility—may help facilitate the evolution of extreme specialization. To see why, imagine a society in which there is caste-based specialization such that (i) a member of one caste cannot perform the tasks for which other castes are specialized, and (ii) each caste has exactly the minimum number of members required for the successful completion of its own specialized task. Such an arrangement would be highly prone to task failure in the face of chance events:

⁷ See Calcott 2008 for a discussion of various ways in which cooperation may generate benefit for group living over social living. One of these ways, “reducing risk”, can be viewed as a form of redundancy; see below.

if a single worker were killed or incapacitated, that worker's caste would no longer be able to function effectively. To secure the robustness of task completion in the face of individual failure, the workforce has two broad options. One is *latent versatility*: if workers of other castes are able to step in to replace their incapacitated colleagues when not required for their own specialized task, task completion will not be imperilled by the failure of a single worker. The other is *redundancy*: if roles are duplicated beyond necessity, or if there are reserve workers on standby, the workforce will again be buffered against individual failure. If a group secures robustness primarily through this second route, the group will be able to sacrifice latent versatility for the sake of more efficient specialization without becoming vulnerable in the face of environmental vicissitudes.

In this sense, redundancy may act as an enabling condition for the evolution of extreme specialization. This conjecture is supported by the correlation between redundancy, specialization and the loss of behavioural totipotency that we see in the eusocial Hymenoptera (Anderson and McShea 2001). Even the largest and most complex colonies, however, retain a large generalist caste of considerable latent versatility (Mirenda and Vinson 1981). For a more extreme data point we can look to paradigm multicellular organisms, which exhibit unparalleled levels of both specialization and redundancy: consider again the example of a red blood cell. In both cases, it seems reasonable to hypothesize that the transition from behavioural totipotency to extreme specialization was accompanied by a transition from robustness-via-versatility to robustness-via-redundancy.

Redundancy is not the sole preserve of eusocial colonies and multicellular organisms. It is also present to some degree in much simpler societies: for instance, animals from the same social group may each hunt independently and share the spoils among their fellow group members (a phenomenon observed in vampire bats; see Anderson and Franks 2001 and

Calcott 2008 for discussion of such cases).⁸ This can be viewed as a very simple form of redundant task structure: the task is to provide sufficient food for the group, and a number of individuals undertake the task in parallel. The benefit, as before, is robustness in the face of individual failure. Complex societies, however, tend to exhibit redundancy to a far greater degree and can achieve a greater degree of robustness as a result; indeed, the degree of redundancy is often so extreme that an individual contribution taken in isolation makes no significant difference at all to the probability of task completion. The difference between simple and extreme redundancy is one of degree rather than kind, and as such is compatible with a gradual transition from simple to complex social organization. As I will argue presently, however, this does not make the evolution of extreme redundancy easy to explain.

The puzzle of extreme redundancy

Acknowledging the proximate aspects of social complexity by no means compels us to deny the SQB thesis. Kin selection theory is not wedded to a pairwise fitness transaction model of cooperation, and its utility is not impugned by the demise of that model. There is no particular reason to think that the core insight of kin selection—the insight that we can explain the stability of cooperation by considering its indirect fitness effects—cannot extend to more complex forms of social interaction. Yet importing old ideas into new explanatory contexts is rarely a straightforward matter. It would be dangerous to simply assume that transitions in individuality pose no special problems at all for kin selection theory, since the distinctive

⁸ Redundancy is also present to a significant degree within the genome, but I will not pursue this interesting analogy here (see, e.g., Thomas 1993, Nowak, Boerlijst, Cooke and Maynard Smith 1997).

features of social complexity may well throw up novel challenges. I want to suggest that extreme redundancy presents just such a challenge.

By way of background, we need to consider how task-based cooperation alters the nature of the dilemma cooperating agents face. Economists have long observed that *social dilemmas*, in which the pursuit of an optimal strategy by each individual leads to an outcome that is suboptimal for the group as a whole, are prevalent in human societies. Such dilemmas can be realized in a variety of ways. In the *tragedy of the commons*, the exploitation of a shared resource by every individual in the group leaves the group with nothing (see G. Hardin 1968). In the *public goods dilemma* or *free-rider problem*, every individual has an incentive to receive the benefits of a public good without contributing to its provision; the danger is that no public good is provided at all (see Olson 1965, Kagel and Roth 1995, R. Hardin 1972, 1980, Medina 2007). The thought that cooperation in *animal* societies might also be usefully studied through the lens of social dilemmas is a relatively recent development, and one that represents a departure from the view that the two-player prisoner's dilemma captures the essence of the problem of cooperation (see, e.g., Hauert, Holmes and Doebeli 2006; Hauert, Michor, Nowak and Doebeli 2006; Rankin, Bargum and Kokko 2007; Killingback, Doebeli and Hauert 2010; Archetti and Scheuring in press).

Task-based cooperation among eusocial insects and somatic cells generates a form of public goods dilemma in which, somewhat counterintuitively, the “public good” is the probability of task completion. In the simplest case, the payoffs of participating (W_P) and free-riding (W_F) will depend on the inclusive fitness benefit to each group member if the task is completed (B), the cost of participating (c), the group size (n), the fraction (\square) of group

members *other than the focal individual* who participate, and the function (f) relating the probability of task completion to the *total* fraction of group members who participate⁹:

$$(1) \quad W_P = B \cdot f(\gamma + 1/n) - c$$

$$(2) \quad W_F = B \cdot f(\gamma)$$

The number and location of the equilibria in such a game will depend, obviously, on the values of B , c and n , and on the nature of the function f . In general, assuming (non-trivially) that there is at least one equilibrium, we can distinguish three broad possibilities:

- (i) If $W_P > W_F$ for all γ , then the only equilibrium is at $\gamma = 0$.
- (ii) If $W_F > W_P$ for all γ , then the only equilibrium is at $\gamma = 1$.
- (iii) If $W_F = W_P$ at $\gamma = \gamma^*$, then a mixed-strategy equilibrium exists at $\gamma = \gamma^*$.

For a plausible illustrative case, we can suppose that f is sigmoidal (i.e., S-shaped): the probability of success is very low when the number of participants is very small, then rises sharply around an inflexion point—a point we may call the threshold of *minimally effective cooperation*—and finally enters a region in which further contributions make little difference. Given that f is sigmoidal, there may be up to two mixed-strategy equilibria, a scenario depicted in Figure 4. In the figure, the equilibria occur at the points of intersection, and the upper point of intersection represents a *stable* equilibrium: when γ exceeds this value, there is an incentive to free-ride; but when γ is approaching this value, there is an incentive to

⁹ In complex societies, the probability of task completion is likely to depend on numerous variables, not just on the overall degree of participation. For current purposes, however, we can assume that all these variables are held fixed, so that the overall degree of participation is the only factor that influences the probability of success. For simplicity, I treat B and c as constants, but in reality both may vary between individuals.

participate. As long as some such equilibrium exists, reasonably high levels of participation may stably coexist with significant levels of free-riding.¹⁰

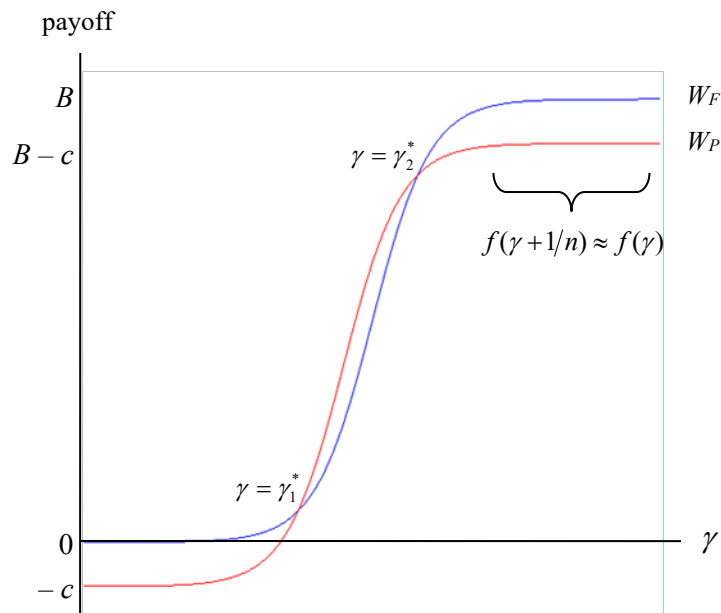


Figure 4. Sigmoidal payoff functions in a public goods game.

Against this background, the puzzle of extreme redundancy rears its head. When redundancy is extreme, the level of participation is so high that a single contribution makes no significant difference to the probability of task completion, i.e., $f(\gamma + 1/n) \approx f(\gamma)$. In Figure 4, this state of affairs corresponds to the upper part of the “S”; we can call this the *extreme redundancy region*. In the figure, the problem is visible at a glance: W_F exceeds W_P throughout the extreme redundancy region; there is therefore an incentive to free-ride whenever redundancy is extreme. Moreover, the figure illustrates a general problem: in a

¹⁰ See Archetti and Scheuring (in press) for a more detailed treatment of public goods games with sigmoidal payoff functions.

public goods game with payoff functions of the general form given in (1) and (2), it will *always* be the case that, if $f'(1/n) > f'(0)$ and $c \gg 0$, then $W_F > W_P$.

In plain terms, then, the puzzle is this: if participating in the task would make no significant difference to the probability of task completion, but the cost of participating remains much greater than zero, then the expected benefit of participating will always be outweighed by the cost. So how do complex societies sustain extreme levels of redundancy? Because this puzzle arises *after* indirect fitness effects are taken into account (recall that B is the *inclusive* fitness benefit of task completion), there can be no prospect of indirect fitness effects straightforwardly dissolving this puzzle in the way they dissolve the prisoner's dilemma. Further explanatory work is needed.

The puzzle may sound familiar: it is structurally similar to the so-called “paradox of voting” in rational choice theory. As Anthony Downs (1957) famously notes, the probability that one's vote will swing the outcome of an election is minuscule; hence, even if the benefits of tipping the outcome would be extremely high, the *expected* benefit of voting will be outweighed by even a small cost (Downs emphasized the costs of following the election closely enough to make an informed choice, but even the utility costs involved in taking the time to vote may well exceed the expected benefit). Yet voters do vote, often in large numbers. This mismatch between theory and data has proved an enduring thorn in the side for rational choice theorists, and the steady stream of proposed solutions continues to this day (see Feddersen 2004 and Dowding 2005 for reviews; see Guerrero 2010 for a recent proposal). The payoff function in the voting case is a step-function rather than a sigmoid, but the analogy with the puzzle of extreme redundancy is close nonetheless.

To briefly sum up: it is widely appreciated that workers in eusocial colonies (and, if the SQB thesis is correct, somatic cells in multicellular organisms) incur huge fitness costs,

often to the extent of sacrificing of their reproductive prospects entirely. This seems puzzling at first glance, but the puzzle vanishes when one considers the expected indirect benefits of cooperating. What is much less widely appreciated is that, owing to the extreme redundancy complex societies contain, individual workers and somatic cells appear to incur huge costs in return for *extremely small* expected indirect benefits. That generates a puzzle that indirect benefits in themselves do not dissipate.

The crane of coercion

The above argument is not intended to show that kin selection theory cannot explain the evolution of extreme redundancy. Indeed, it is hard to imagine how any consideration could support such a strong negative conclusion. The puzzle of extreme redundancy does, however, suggest something interesting about the *order* in which the proximate aspects of social complexity arise in the course of a fraternal transition. For it gives us reason to suspect that extreme redundancy is unlikely to evolve as long as the personal fitness difference between participating and free-riding remains significantly greater than zero. Recall the structure of the argument: when redundancy is extreme, a single worker (or somatic cell) makes no significant difference to the probability of task completion. Hence, as long as there is a significant fitness cost attached to participating, the worker always has an incentive to free-ride.

To solve the problem, we need a further mechanism that negates the personal fitness difference between participating and free-riding, and hence eliminates the incentive to free-ride even when one's contribution to the probability of task completion is insignificant. We see a plausible mechanism in the eusocial Hymenoptera in the form of *coercion* or *worker policing*, whereby, in some colonies, around 98% of worker-laid eggs are eaten by the queen or by other workers (see Ratnieks and Wenseleers 2008). This relatively simple social

behaviour (it is, in Anderson, Franks and McShea’s scheme, a mere “individual task”) can be straightforwardly explained by kin selection theory, since haplodiploidy ensures that workers are more closely related to the offspring of the queen than to the offspring of their fellow workers—and so have an inclusive fitness incentive to help the queen reproduce at other workers’ expense (Ratnieks 1988).

There are two ways to interpret the effect of coercion on the public goods game of task-based cooperation. We could say that the effect of coercion is to reduce the cost of participation (c), or we could alternatively say that, though c remains high, policing imposes an additional cost (d) on those who attempt to free-ride. The choice makes no difference to the dynamics, and depends only on what we take a worker’s baseline fitness (i.e., their fitness less the effects of social interactions) to be. My preference is for the second option: participating in collective tasks intuitively entails a cost to the viability and fecundity of a worker, and the effect of coercion is to impose a counterbalancing cost on those who attempt to free-ride. On this interpretation, coercion leads to the modified payoff functions:

$$(3) \quad W_P = B \cdot f(\gamma + 1/n) - c$$

$$(4) \quad W_F = B \cdot f(\gamma) - d$$

If $c = d$, then $W_P > W_F$ even if $f(\gamma + 1/n) < f(\gamma)$. Participation will be an evolutionarily stable strategy, and there will be an incentive to participate even when redundancy is extreme. I suggest, moreover, that $c = d$ is a reasonably plausible interpretation of the scenario we see in societies with effective coercive regimes. In such societies, coercion counterbalances the cost of participation, such that the chance a worker has of getting its genes into the next generation by a direct route is unaffected by whether or not it chooses to participate in collective tasks. Either way, the chance is effectively zero. These, I suggest, are the ecological conditions in which extreme redundancy can evolve.

While the role of coercion in resolving reproductive conflict in insect societies has been well documented in recent literature (see Ratnieks, Foster and Wenseleers 2006 for a review), this hypothesis highlights the potential *creative* role of coercion as an enabler for the evolution of further aspects of social complexity—aspects which, on the face of it, have little to do with the policing of egg-laying, but which would not be stable in its absence. When an effective coercive regime is in place, large numbers of workers may stably participate in large-scale cooperative tasks even when the expected inclusive fitness benefit conferred by their own individual contributions is extremely small, because the cost of participating is fully counterbalanced by the costs imposed on free-riders. The effect of systematic coercion is thus to modify the selective environment in such a way as to make the evolution of extreme redundancy possible. Extreme redundancy, for its part, then helps enable the evolution of the extreme specialization characteristic of transitions in individuality.

If this hypothesis is on the right lines, the story that emerges is one in which kin

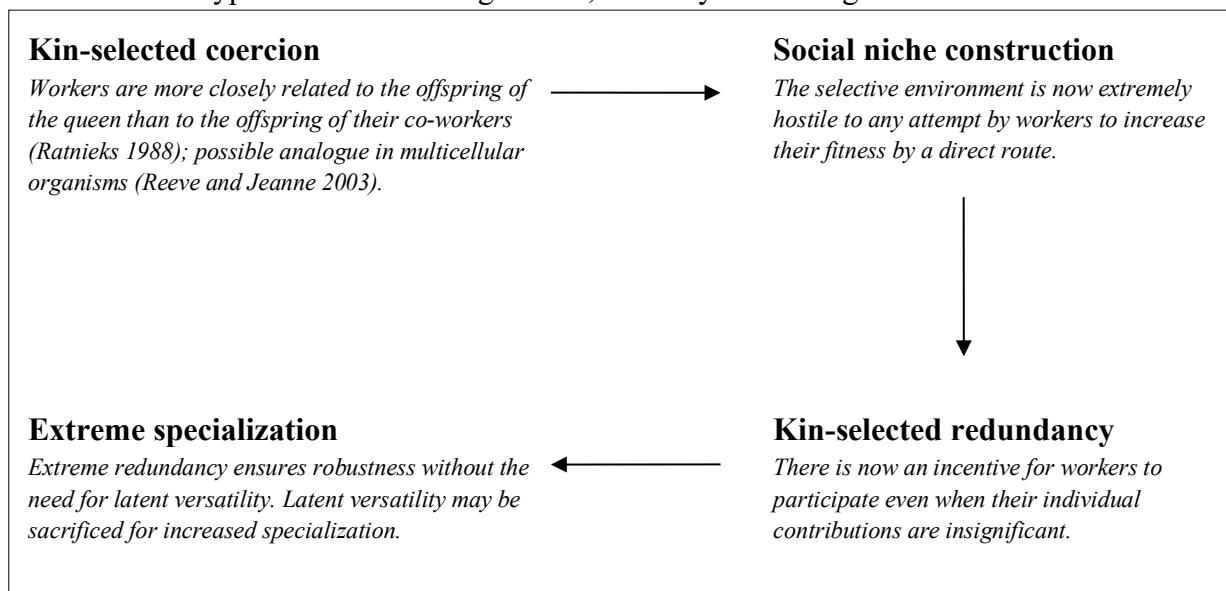


Figure 5. The “crane of coercion” hypothesis

selection is indeed the driving force in the evolution of extreme redundancy and specialization, but in which it is not the *only* cause that matters. Instead, we have a four-step mechanism (Figure 5). In the first step, kin selection favours coercive behaviour among the

lower-level entities, imposing a cost on workers who attempt to reproduce. Coercion results in a selective environment that is extremely hostile to any attempt by a worker to increase its inclusive fitness by a direct route; by contrast, a behaviour that increases inclusive fitness by an indirect route will be favoured even when the expected benefit it confers is extremely small. This second step is, in a manner of speaking, a form of *niche construction* (sensu Odling-Smee, Laland and Feldman 2003), but it is the *social* environment rather than the natural environment that has been altered.¹¹ In the third step, further kin selection in the modified selective environment generates complex task-structures characterized by extreme redundancy. Finally, extreme redundancy enables the loss of latent versatility for the sake of increased specialization.

Could a similar mechanism explain the evolution of extreme redundancy and specialization in multicellular organisms? As H. K. Reeve and R. L. Jeanne (2003, p. 1044) note, mutations during mitotic cell division can generate considerable genetic heterogeneity in multicellular organisms, and this heterogeneity implies scope for reproductive conflict (see also Buss 1987, Michod 1999, Bourke 2011). Reeve and Jeanne proceed to argue that cell lines will have an incentive to coerce one another, leading to a scenario in which reproductive capacity is largely concentrated in a single dominant cell line. This will be the slowest-dividing cell line, for this is the cell line to which the others have the highest mean relatedness. The upshot is an enforced germ-soma separation in which the reproductive potential of the somatic cell lines is highly constrained; apoptosis among somatic cells may subsequently evolve as a form of self-restraint. We see a similar form of self-restraint in the eusocial insects, where workers, despite being able to activate their ovaries and produce male

¹¹ I borrow the term “social niche construction” from Powers, Penn and Watson (2011), who apply it in a rather different context.

eggs, tend to do so *extremely* rarely: this restraint may plausibly have evolved as an adaptive response to the near impossibility of successfully protecting one's eggs (Ratnieks and Wenseleers 2008). These are speculative remarks, and there is evidently a need for further investigation. Nevertheless, we can conjecture that the coercion of free-riders may be of general importance in driving fraternal transitions.

4. The fate of the SQB thesis

Much of the foregoing discussion is highly sympathetic to the SQB thesis. In Section 2, we canvassed several aspects of complex sociality (namely, the task structure of cooperation, plus four further features that add to its complexity). Two general morals leap out from this survey. First, many of the organizational features of eusocial colonies are shared, in some form or another, by paradigm multicellular organisms. Second, the same features are also exhibited, albeit to a much lesser degree, by many simpler animal societies. The overall picture is one in which the same broad types of social phenomena are found throughout the biological hierarchy, recurring wherever groups of entities are bound into stable, integrated wholes. Yet these features also represent departures from a traditional conception of cooperation as a pairwise interaction between individuals. The demise of the pairwise fitness transaction model, while not incompatible with the SQB thesis, generates new explanatory challenges for the study of social evolution.

In Section 3, we considered in detail one aspect of social complexity (namely, extreme redundancy) and the distinctive explanatory challenge it presents (namely, a biological analogue of the paradox of voting). The puzzle of extreme redundancy threatens a very strong reading of the SQB thesis according to which transitions in individuality are alleged to present no special problems at all for kin selection theory, but it seems doubtful that

anyone would seriously defend so strong a reading. The “crane of coercion” hypothesis supports a more modest reading of the SQB thesis on which kin selection, as part of a complex multi-step process, and in conjunction with other evolutionary processes such as niche construction, is indeed pivotal in driving the evolution of extreme redundancy and the extreme specialization it may facilitate. The general moral, I suggest, should be one of qualified optimism. Kin selection theory may well turn out to explain far more than it was originally designed to explain. If the case of extreme redundancy is indicative of a broader trend, however, it will do so only as part of an integrated theoretical framework that recognizes both the special problems posed by transitions in individuality and the distinctive mechanisms by which these problems may be overcome.

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