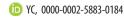**Author for correspondence:**
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Operationalizing evolutionary transitions in individuality

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Evolutionary transitions in individuality (hereafter, ETIs), such as the transition to multi-cellularity and the transition to social colonies, have been at the centre of evolutionary research, but only few attempts were made to systematically operationalize this concept. Here, we devise a set of four indicators intended to assess the change in complexity during ETIs: system size, inseparability, reproductive specialization and non-reproductive specialization. We then conduct a quantitative comparison across multiple taxa and ETIs. Our analysis reveals that inseparability has a crucial role in the process; it seems irreversible and may mark the point where a group of individuals becomes a new individual at a higher hierarchical level. Interestingly, we find that disparate groups demonstrate a similar pattern of progression along ETIs.

1. Introduction

The emergence of novel levels of individuality is a recurrent theme in the history of life. Biological units that previously existed as independent individuals are incorporated within a higher level of organization, which becomes a new individual [1–8]. For example, multi-cellular organisms comprise cells whose ancestors were individual unicellular organisms [3,9,10]. Another example is the transition of individual organisms into a social colony, as illustrated by all ants and some bees (and a handful of other eusocial species). The whole colony is arguably a single individual, and the ants or bees can be viewed as the mobile equivalents of cells in an organism [11,12]. Two crucial features justify the labelling of these insect colonies as a kind of individual. First, a single ant could not survive on its own, not even the queen. Only the colony as a whole is capable of survival and reproduction. Second, the vast majority of the colony members do not reproduce. Here, we concern only those evolutionary transitions in individuality (hereafter, ETIs) where the lower-level units belong to the same species ('fraternal transitions' *sensu* Queller [13]).

A common feature of ETIs is that, as the division of labour within the newly established higher-level organism develops, its lower-level units become more specialized, and lose much of the capabilities and behavioural repertoire of their free-living precursors, as shown for ant castes [21], for zooids in marine invertebrate colonies [22] and for metazoan cells [23]. Many ETIs from independent multi-cellular organisms into fully integrated colonies are found in a range of marine invertebrate taxa (e.g. corals, hydrozoa, bryozoa and tunicates [14]). The diversity of internal structure and function within this group attracted zoologists to distinguish stages in the transition 'from aggregates to integrates' (*sensu* Thomson & Geddes [15]) within these phyla; alternative 'colony individuality' scales were proposed [1,15,16]. The view of the integrated colony as a higher-level individual [1,14–18], as well as the parallels between marine invertebrate colonies and social insects [18–20], were noted long ago.

(a) Defining individuality

The concept of biological individuality and the physical organization and dynamics it denotes have been debated among scientists and philosophers for centuries, from Aristotle's *Parts of animals* [24] to Leibniz's 'monad' (explained in [25])

and Wilson's 'biological individuality' [26]. Some aspects of these aforementioned debates found their way to discussions of ETIs [27,28], such as the major division between functional and evolutionary definitions of an 'individual' [29]. Functional definitions focus on physiological aspects of the individual as a distinct, well-delineated and cohesive unit. Functional individuality focuses on the question of unity: how do distinct components constitute a cohesive unified whole, functioning collectively as a single and regulated unit that persists through time [29,30]? Individuality is often defined in an evolutionary context [17,31,32]. In this context, an individual is a unit characterized by its capability to reproduce [33], and by its degree of heritability and fitness [31], with a possible extension to multi-level selection perspective [34]. Some evolutionary views of individuals focus only on one aspect, such as individuals as replicators [35], or individuals as interactors [27,34]. A special class of views concerns individuals as interactive parts of a collective system—including a developmental system [36,37], an ecological niche [38] and a holobiont [39]. Queller & Strassmann define an organism as a unit with high cooperation and very low conflict among its parts [40]. Other approaches to individuality also exist [41,42]. For the purpose of the current discussion, an individual is defined here broadly as a unique entity that is capable of autonomous survival and reproduction. This definition is meant to serve as a convenient and tentative proposition; it combines functional and evolutionary elements. It follows from this definition that individuality may appear simultaneously in more than one hierarchical level (such as in the organism and its cells [31,32,41]). Also, it should be noted that individuality is a quantitative trait [43] rather than a binary (present or absent) trait. We realize that this definition is too narrow to capture all aspects of individuality, and too vague to be useful in precise mathematical models or philosophical definitions, but we believe it is a useful definition in the context of ETIs. A comprehensive understanding and integration of the various facets of individuality is yet to be developed [41].

(b) Social evolution and evolutionary transitions in individualities

How these transitions came to be is a matter of much engagement and debate. A central question concerns the problem of individuality in the sense of multi-cellular organisms: organisms live to reproduce, and giving up prospects of reproduction contradicts the organism's most basic interests [44]. In Maynard Smith's words, 'How did natural selection bring about the transitions from one stage to another, since at each transition, selection for "selfishness" between entities would tend to counteract the change … how is it that selection at the lower level does not disrupt integration at the higher level?' [44]. In view of this difficulty, several explanations were proposed, based on conceptual descriptions [9,10,28,34,45], on empirical observations and experiments, mainly on volvocine algae [46,47], and on mechanistic mathematical models [48,49]. The relative weight of kin selection versus group selection is still hotly debated.

The inclusive fitness theory [50] along with its many adjustments and applications for the praxis of scientific modelling is currently one of the most widely accepted explanations of social behaviour in general [51,52], including the change in individuality that occurs through major evolutionary transitions [9,45,53]. An ongoing debate is the role of genetic relatedness between colony members in the transition process;

more specifically, the question raised is whether genetic relatedness causes [45,54] or is a consequence of [55] ETIs to sociality. Some researchers suggest that in the initial phases of sociality in insects, group selection was crucial [55,56], and others maintain that kin selection played an essential role in the formation of insect societies [45,57]. Yet most researchers agree that the mathematical models of kin and group selection are mutually translatable [58], while differences concern the spatial and genetic setting within and between organisms [51,56]. It is difficult to obtain evidence of processes that started 10^7 years ago and continued for 10^6 years or more (but see [59] for an indication of strong group selection in the early stages of the transition to multi-cellularity). In general, it seems that the transition to a stable social group requires that the individuals that form it must inherit the same behavioural information; this information need not be transmitted through DNA; it can also be transmitted through social learning [60,61]. A separate debate concerns the proposition that ETIs resulted from non-selective forces [62–64]). Our goal here is not to investigate mechanisms, but rather to propose a systematic method to quantitatively evaluate ETIs, and compare between them. We wish to characterize the fuzzy concept of ETI using a set of measurable criteria, or, in other words, to operationalize ETIs.

(c) Operationalizing transitions in individuality

Operationalization of ETIs may serve at least two goals: (i) it is a prerequisite for achieving a quantitative understanding of ETIs and the factors affecting them and (ii) it may enable concrete comparisons between different ETIs. Using a set of measurable parameters will make it possible to identify and evaluate biological entities in terms of their degree of change along the transitional stages between one level of individuality and another. Hence, the goals of this study were (i) to propose an operationalization scheme for ETIs based on a concise and robust set of complexity indices and (ii) to apply this operationalization scheme to groups of extant organisms at various stages along a transition, and use the results of this exercise to compare patterns of change during ETIs between these groups and between two ETI types.

Some comparative studies of ETIs classify transitions arbitrarily into two or three stages [9,28,45,65]. Few attempts were made to study ETIs using a predefined set of quantitative parameters (=to operationalize ETIs) [5,7,66]. McShea [7,12,67] proposed to characterize ETIs using vertical complexity (*sensu* Sterelny [68]), recording the number of nested hierarchical levels present in an organism, and 'horizontal complexity' that determines the degree of individuation for the top hierarchical level. For horizontal complexity, Mcshea [7,69] proposed three parameters (connectedness, differentiation and existence of intermediate parts), of which we adopt connectedness and differentiation. Queller & Strassmann [40] proposed a plane that represents the level of organismality, whose axes are the level of cooperation and the (inverse of) level of conflict. Recently, Hanschen *et al.* [66] proposed an operationalization scheme that characterized individuality based on eight parameters, targeting specifically the transition to multicellularity, and applied to the volvocine group as a case study. We adopt here two of their parameters, namely reproductive division of labour, and inseparability. Two other criteria, genetic uniqueness and genetic homogeneity, do not change during volvocine transition [66]. Two additional criteria proposed by Hanschen *et al.* [66] were that the higher

hierarchical level is characterized by physiological unity and integration, and by spatio-temporal boundaries; these two criteria fit the transition to multi-cellularity, but application to insect social colonies is difficult since lower-level units are motile. Finally, two other criteria, group-level adaptations and multi-level selection, are valuable as indicators of ETIs in general; yet we did not include them in our scheme since they cannot be estimated directly but rather inferred from other observable phenomena. Thus, our scheme for operationalizing ETIs combines elements from the schemes of McShea [7] and of Hanschen *et al.* [66].

Many scholars discuss the relations between evolution and complexity, particularly in the context of ETIs, for example [3,5,6,64,67,70]. Apparently, ETIs are characterized by increasing complexity along most of their various stages [3,6,70]. We therefore organize our scheme for operationalizing ETIs around the concept of complexity, based on the assumption of an increase in complexity during an ETI. We hypothesize that an operationalization scheme based on a concise set of robust parameters may yield meaningful insights on processes that are common across different evolutionary lines and even across different ETI types. The parameters selected for our scheme had to satisfy three criteria: (i) be general and applicable to any ETI, (ii) could be robustly estimated for various taxa, and (iii) cover a unique type of complexity, unaccounted for by other parameters.

2. Methods

Combining elements from the schemes of McShea [7], Herrera-Paz [71] and Hanschen *et al.* [66], we propose that four parameters can serve as a general operationalizable set for measuring complexity in biological systems: (i) the number of levels in a system [7,71], (ii) the number of units in a level [67,72], (iii) the number of different types of units, or the variation between units [71,73], and (iv) the connectivity between units [71].

Each of these parameters represents an independent concept [67]. Taken together, they capture, at least partially, the elusive and multi-faceted notion of complexity in biological systems. However, adjustments are required when adapting this set to any specific circumstances. In the case of major transitions, the following adaptations are needed: the first above-mentioned parameter, i.e. the number of levels in the system, is not relevant to our purposes, since this study concerns only two hierarchical levels that mark the beginning and the end of the transition. Hence, in our scheme, the first parameter is the *number of* lower-level units (indicative of the size of the system). Examples of this parameter are the number of cells in an organism, or the number of organisms in a social colony. The next of the above-mentioned parameters, connectivity between components, is difficult to quantify directly; following [66], we propose *inseparability*, which is an aspect of connectivity, as a corresponding complexity measure in the proposed operationalization scheme. Finally, the variation between units in a system was evaluated in our scheme using two separate parameters: reproductive specialization [66] (e.g. the distinction between somatic cells and gametes, or between workers and queen) and non-reproductive specialization [7] (e.g. the distinction between various tissues in an organism). We separated these two types of specialization because they can appear at very different stages during a transition and thus could be indicative of different degrees of complexity along the ETI continuum. Non-reproductive specialization can be quantified as a continuous variable, using the number of unit types as an indicator (e.g. the number of cell types). This measure of the variation between units has been commonly used to quantify complexity in living

systems [64,72,74], in spite of conceptual and technical issues, that were only partially solved [75]. While useful in documenting the increased complexity during advanced stages of individuation, it is less informative in the context of the critical stages of an ETI, when the new hierarchical level is being established. We thus do not include the number of unit types in our scheme.

In the present study, the size of the system was considered a continuous variable. For the three other parameters—inseparability, reproductive specialization and non-reproductive specialization—estimating a specific continuous value across taxonomic groups and transition types is highly uncertain, given the present state of our knowledge. Thus, these parameters were recorded as present or absent, making our operationalization method inevitably imprecise. Our scheme is evaluated using a relatively small number of extant taxa and ETIs, and is thus incomplete. Future studies may improve both the precision and completeness of our work.

(a) *System size* (the size of the individual) is the number of units within a given system; for example, the number of cells in an organism or the number of individual organisms in a eusocial insect colony.

(b) *Inseparability* is the incapacity of some of the system's components (cells, individuals, subgroups) to survive and complete their life cycle separately, independent of the more complex (higher-level) entities (e.g. the organism when separated from the colony). Ideally, this measure could be a continuous variable between zero and unity. However, inseparability is a binary variable here: very low probability (or frequency) of independent survival of lower-level entities is interpreted as complete inseparability; otherwise, complete separability (zero inseparability) is inferred.

(c) *Reproductive specialization* means that only certain units of the system (cells in an organism/individuals in a colony) specialize in reproduction. Here, reproductive specialization is marked as present when some units are capable of reproduction, while other units are entirely and irreversibly incapable of reproduction.

(d) *Non-reproductive specialization* is the variability among units that is unrelated to reproduction. In an organism, it is the degree to which different cells specialize in different non-reproductive tasks. This feature is considered present if there are at least two distinct somatic cell types. In eusocial organisms, it is considered present if there are at least two types of non-reproductive morphs.

(a) Application to two types of evolutionary transitions in individualities

We applied this operationalization scheme to characterize the location of specific taxa along an ETI. We looked for taxa that could be grouped together coherently, in order to characterize intermediate stages along a major transition. Extant organisms representing intermediate stages of a transition pertain to only two types of ETI: the transition to multi-cellularity and the transition to eusociality. Both transitions are fraternal (*sensu* Queller [13]); the new higher-level individual is composed of similar and related units. The term 'intermediate' does not imply that these intermediates are precursors of other organisms along a transition. Rather, we presume that intermediates possess only some of the characteristics of an organism that has completed the transition.

A taxon was added to table 1 if it satisfied two conditions: (i) it differs in at least one feature from all other records in its group already existing in the table (the rationale for this condition is to avoid inflating the table with records that are identical for all columns except the name of the species); and (ii) enough data exist to reliably classify that taxon in all criteria.

Table 1. Complexity indicators applied to various organisms in three general groups. Description of table columns appears at the beginning of the Methods section. Rows of the table are ordered by system size.

general group	case studies	system size (size of the colony)	inseparability[a]	reproductive specialization[b]	non-reproductive specialization[c]
(a) volvocine algae					
	Tetrabaena[d]	4	−	−	−
	Gonium sp.[e]	4–32	−	−	−
	Pandorina[e]	8–16	+	−	−
	Eudorina[e]	32–64	+	−	−
	Pleodorina[e]	128	+	+	−
	Volvox[f]	10^4	+	+	−
(b) partial multi-cellularity					
	Choano-flagellates[g]	10^0 (10^2)	−	−	−
	dictyostelid slime moulds[h]	10^0 (10^6)	−	−	−
(c) Metazoa (animals)					
	nematodes[i]	10^3–10^4	+	+	+
	tardigrades[j]	10^3–10^5	+	+	+
	Placozoa[k]	10^7	+	+	+
	sponges[l]	10^{10}–10^{12}	+	+	+
	mammals[m]	10^{10}–10^{15}	+	+	+
(d) social colonies[n]					
	allodapine bees[o]	10^1	−	−	−
	halictine bees[o]	10^2	−	−	−
	naked mole rats[p]	10^2	−	−	−
	social spiders[q]	10^2–10^3	−	−	−
	bumblebees[r]	10^2	+	+/−	
	polyembryonic wasps[s]	10^2–10^3	+	+	+
	Vespinae wasps	10^3	+	+	
	honeybees	10^4–10^5	+	+	−
	termites[t]	10^2–10^6	+	+	+/−
	ants[u]	10^2–10^9	+/−	+/−	+/−

[a]In social colonies, inseparability is inferred when queen-replacement is not possible.

[b]In social colonies, reproductive specialization is inferred from the degree of queen–worker caste dimorphism and presence of sterile workers [45].

[c]In social colonies, non-reproductive specialization is inferred from worker polymorphism.

[d]Information on size, inseparability, and specialization of Tetrabaena was derived from [76].

[e]Information on Gonium, Pandorina, Eudorina and Pleodorina was derived from [77].

[f]Size: up to 3000 for Volvox carteri [46] and up to 50 000 for Volvox sp. [78]. Information on inseparability and specialization of Volvox was derived from the same references.

[g]Choanoflagellates may readily switch between unicellular and multi-cellular forms [79]; information on Choanoflagellates was derived from [79–81].

[h]Slime moulds are solitary in part of their life cycle; the number of cells in fruiting bodies is between 10 000 and 2 000 000 [82]. Some cells that do not aggregate still survive, and may recover when conditions improve [83], implying that aggregation is not mandatory for survival, and hence no inseparability (but see [18]). During the aggregation phase, some of the cells form the stalk, while others become spores [82]; yet, each cell has the potential to become either stalk or spore [84], and hence no reproductive specialization is implied.

[i]Information on size, inseparability and specialization of nematodes was derived from [85].

[j]Information on size, inseparability and specialization of tardigrades was derived from [86].

[k]Average cell size of Trichoplax is approximately 10 µm, body size approximately $2 \times 3 \times 0.015$ mm [87], yielding approximately 10^8 cells. There is some evidence of bisexual reproduction [87,88], and six different types of somatic cells were found in Trichoplax [89], hence reproductive and non-reproductive specialization are inferred.

[l]Sponges are a diverse group with a large range of body sizes (10^{10}–10^{13} cells per individual; G. Yahel and S. Leys 2019, personal communication). They have a complex body plan; a single somatic cell cannot regenerate to reconstruct a whole sponge, inferring inseparability [90]. They have separate germ- and somatic cell lines, and six distinct somatic tissues [91], inferring reproductive and non-reproductive specialization.

[m]Estimate of mammal body size is based on the number of cells in a human body, approximately 3×10^{13} [92,93], considering that mammal sizes vary over eight orders of magnitude, and cell sizes vary over one order of magnitude.

(Continued.)

Table 1. (Continued.)

[n] Data on eusocial colonies are based on table 1 in [94], except where stated otherwise.

[o] In allodapine and halictine bees, an incomplete reproductive specialization exists, where workers may produce eggs in some circumstances [94,95].

[p] In naked mole rats, reproduction is typically monopolized by a single queen in colonies of 100–300 individuals [96,97]. A queen can be replaced by any of the workers [98]. In spite of some task specialization, task switching is common [99], and in spite of size heterogeneity, there are no castes [100,101].

[q] There are no known species of spiders with inseparability or specialization [102].

[r] The queen bumblebee is the sole producer of gynes, while queen and workers produce males [103]; reproductive specialization is therefore incomplete.

[s] Polyembryonic wasps are found in four families with diverse traits. Here, we follow *Copidosoma floridanum* [104,105]. Colony size of larvae within host varies between 40 and 1200 [105,106]. Inseparability is inferred since small colonies (less than 600) do not survive in host [104]. Brood includes two castes of soldiers that do not reproduce, indicating both reproductive and non-reproductive specialization [105].

[t] Data on termites taken from [107–110]. All termite species have sterile soldier castes, rendering them reproductive specialization [110], but not all species have sterile workers, thus non-reproductive specialization do not occur in some species.

[u] Ant colony size varies largely, with megacolonies of some species contain up to 10^9 ants [111]. There are corresponding variations in the other traits as well [94,112,113], see text for details.

The volvocines form 'a league of their own', with several species at various stages of 'embryonic' multi-cellularity [46,78]. Thus, the volvocines are treated here as one general group (table 1a). A second group consists of two organisms that are on the verge of multi-cellularity: slime moulds, who live most of their life cycle as unitary cells, but may aggregate and form multi-cellular reproductive structures [82–84,114], and Schoanoflagellates, that may readily switch between a unitary cell and a colony (table 1b). A third group, the metazoan, consists all animals (table 1c). All animals possess inseparability and both forms of specialization. We selected five organisms that differ markedly in size. Nematodes and tardigrades, in spite of their miniature size, have tissues and organs. Placozoa is a basal group of multi-cellular animals that lack organs and internal structure [88,115,116]. Recent studies provided conflicting evidence regarding the origins of Placozoa, being either distant to all other animals [115] or closer than sponges to other animals [116]. Sponges are often considered the most primitive multi-cellular organisms. Mammals represent taxa that developed relatively recently. In spite of 1.4 billion years of divergence, all these organisms are thought to have originated from the same transition to multi-cellularity.

Plenty of formations that correspond to intermediate stages of the transition to eusociality currently exist. We selected seven different taxa as case studies for the transition to eusociality (table 1d). We follow definitions and specific examples in table 1 of Bourke's 'Principles of social evolution' [45].

The large group of colonial marine invertebrates was omitted since an entire article would be required to seriously cover its great taxonomical, structural and functional diversity; thus, their inclusion would render this paper a zoological survey rather than a conceptual proposition.

3. Results and discussion

We propose a simple and general scheme to operationalize the concept of evolutionary transitions in individuality (ETI). Our aim here is to quantify the multi-facet concept of complexity (rather than individuality) during these transitions. Some general features in the progression of ETIs emerge from our analysis. System size increases across many orders of magnitude. The profound relations between system size and complexity were discussed before, concerning the inherent jump in organism size following a major transition [117] and concerning the increasing complexity within the top hierarchical level with increasing size [72,118–121]. There appears to be a strong relationship between system size and each of the other complexity parameters. For volvocine algae, for example, there are strong positive relations between the number of cells

and soma/germ ratio [122]. Colony size is positively related to both reproductive specialization and non-reproductive specialization [94,112,119]. The relations between colony size and reproductive specialization were found to be related to the capacity for motility of the colony [123]. In our study, the relations between size and other indicators of complexity are demonstrated by the pattern of +/− signs that emerges in table 1. Once a specific parameter (inseparability, reproductive specialization or non-reproductive specialization) appears in an organism, it also appears in all larger organisms within the same general group (table 1). The only exception to this rule is the presence of non-reproductive specialization in polyembryonic wasps (table 1d). If the relationship between system size and each of the other parameters was weak or non-existent, then the vertical sequence of +/− signs in each column in table 1 would be random; as this sequence is perfectly ordered, it appears that the size of a biological system is an important predictor of the location of that system along an ETI. Previous studies proposed that the size of a colony is a major driver of the transition to multi-cellularity [4,72] and to eusociality [94]; here, we found a strong and general empirical pattern that seems to confirm their hypothesis. Size does not relate linearly to time; however, it is plausible that smaller systems appear earlier than larger systems, and thus, it may be assumed that typically, the order of appearance of systems is correlated with system size (but see [124,125] for special cases that reveal an opposite trend).

With the increase in system size, the three other complexity indicators appear gradually, in a similar (but not identical) order (table 1): in all groups, inseparability and reproductive specialization appear rather early (in systems of 10^2 units). In volvocine algae, inseparability appears before reproductive specialization, while in social colonies, they appear together. By contrast, non-reproductive specialization appears much later (in systems greater than 10^6 units). This pattern is repeated in the two types of ETI, suggesting that even this preliminary operationalization yields insights into the general causal *processes* that produced major evolutionary transitions.

Within the animal kingdom, we found two exceptions to this rule, nematodes and tardigrades. These are fully fledged organisms with 10^3–10^5 cells only. It is possible that they originated from much larger organisms, following an evolutionary process of size decrease, which is typical in parasites [125]. Similarly, parasitic multi-embryonic wasps are a single exception to this rule among social colonies. Ants and termites are two groups of numerous species, with colony sizes from

dozens to millions (termites) or even billions (ants). Corroborating results of this study, colony size in these groups was found to be strongly correlated with inseparability, reproductive specialization and non-reproductive specialization [94,112,113]. A full account of the variability in these two groups is beyond the scope of this article.

Inseparability, the incapacity of single units to regain independence, is found even in an organism as simple as the 16-cell algae Pandorina. It is found in all larger algae, and in all extant multi-cellular organisms. Inseparability also appears in all insect colonies larger than 10^2. Michod [9] claims that 'Reproductive specialization is a major factor in the conversion of cell groups into true multi-cellular individuals. Once cells specialize in fitness components, they cannot survive and reproduce on their own; the group becomes indivisible, and hence, an individual'. We fully agree with Michod [9] that inseparability marks the stage in which a group of lower-level units becomes a higher-level entity (individual). Once inseparability is achieved, heritability and variation are automatically transferred to the higher level; selection at the lower level is meaningful only in the context of the newly established individual; the fate of this individual becomes the only determinant of the survival and fitness of each lower-level unit. Thus, inseparability seems to play an important causal role in driving an ETI from a collection of individuals into a new collective level of individuality. Inseparability was used to define a transition in the book on major transitions [6], but the view of inseparability as a causal driver of the transition was seldom mentioned in evolutionary transition models. A second proposition in the above quote is that reproductive specialization translates inevitably to inseparability, since specializing cells cannot survive on their own. We agree that reproductive specialization must result in inseparability, except in cases where inseparability precedes reproductive specialization; our survey here did not reveal any such example, but human societies may exemplify this possibility [126]. In social colonies, incomplete inseparability (a worker may become a queen in rare occasions) and incomplete reproductive specialization are present in mole rat colonies [96–98], suggesting that a possible positive feedback loop between these two elements may have driven transitions forward to the irreversible point of complete inseparability. Therefore, we suggest that inseparability is better understood as a causal facilitator of reproductive specialization rather than its byproduct.

The early appearance of inseparability, as observed here, suggests that the issue of cheating does not necessarily play a crucial role in ETIs. During a transition, if enough units act as free-riders, it may dissolve the emerging cooperative system, yet cheating becomes more risky and less likely if the cheater cannot survive alone. Thus, our findings support Calcott's claim [127], that too much of the science of social evolution concerns the problem of cheating. Once inseparability is attained, the fitness of cheating individuals essentially corresponds to the fitness of the new, higher-level individual, and the advantage gained through cheating behaviour is either neutralized or becomes a disadvantage. There are other crucial issues that need to be resolved in order for the prospective entity to survive, chiefly the synchrony of replication [3,6,128,129]. Once inseparability is established, a massive selection pressure develops towards solving these conflicts. Selection pressure towards replicative synchrony is perhaps indicated by the fact that most cancer types develop at old age, where selection pressure resulting from replicative a-synchrony is low.

Reproductive specialization precedes non-reproductive specialization in all the groups inspected here. Necessarily, if non-reproductive specialization developed prior to reproductive specialization, it would at some point inflict some reproductive specialization as well, since modifications in structure and function of lower-level units affect their fitness.

4. Conclusion

This study proposes a general scheme, applicable to fraternal transitions in individuality, based on four independent parameters, indicating four aspects of complexity. Applying this scheme to different groups and ETI types, we found a consistent sequential chain of events. Inseparability appeared in all cases either before or together with reproductive specialization, indicating its crucial role in the process; it marks the turning point where a group of individuals becomes a new individual of a higher hierarchical level; moreover, by tying together the fitness of all inseparable lower-level units, and assigning it to the fitness of the newly emerged higher-level individual, inseparability dictates conflict resolution and may be major driving force through the transition. This paper shows that operationalizing ETIs makes it possible to compare different systems within the same transition type, as well as different transition types, yielding new and important insights. Finally, such operationalization allows us also to evaluate additional questions in a new way, such as the specific case of humanity in the context of ETIs [126].

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