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From asexual to eusocial reproduction by multilevel selection by density-dependent competitive interactions

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Abstract A game theoretical model is developed to illustrate that multilevel selection by density-dependent competitive interactions in mobile organisms might have played a major role in the evolutionary transitions from asexual over sexual to eusocial reproduction. The model has four equilibria with selection occurring among interacting units of respectively one, two, three and up to infinite many individuals. The different equilibria are characterised by different levels of competitive interactions among interacting units, and these levels select for different levels of sexual and co-operative reproduction among the individuals of the units. The model predicts: (*i*) that low-energy organisms with negligible body masses have asexual reproduction, (*ii*) that high-energy organisms with non-negligible body masses in evolutionary equilibria have sexual reproduction between a female and a male, (*iii*) that high-energy organisms with non-negligible body masses that increase exponentially at an evolutionary steady state have co-operative reproduction between a sexual pair and a single sexually produced offspring, and (*iv*) that high-energy organisms with upward constrained body masses have eusocial reproduction between a sexual pair and up to an infinite number of sexually produced offspring workers.

Keywords: Competitive interactions, density dependence, multilevel selection, major transitions, sexual reproduction, eusocial colony, life history evolution.

Contents

1 Introduction

During evolution on Earth there have been transitions toward reproductive units of ascending inclusion, where higher-level units arise from co-operative reproduction among lower-level units (Vrba and Gould 1986; Buss 1987; Maynard Smith and Szathmáry 1995). At the lowest level the reproductive unit is formed by the asexual self-replicators, that are considered to define the origin of natural selection (Michod 1999; but see Lifson and Lifson 1999). At higher levels the reproductive unit can take the form of a cell, a multicellular organism, or a group of multicellular organisms, with groups including sexual pairs, co-operative breeders, and eusocial colonies.

As defined by interactors, or interacting units, natural selection is a second dimension that exists in a multilevel hierarchy that resembles the hierarchy of reproductive units (Hull 1980, 1981; Brandon 1988; Wilson

and Sober 1994; Lloyd 1988; Sober and Wilson 1998; Gould and Lloyd 1999; Keller 1999). At the lowest selection level interactors are given by the hereditary material. For self-replicators at the origin of life, with no distinction between genotypes and phenotypes (Michod 1983, 1999; Szathmáry and Maynard Smith 1997), the lowest interacting level is the self-replicator itself. For higher organisms, with genotypic and phenotypic distinction, the lowest interacting level is the gene, which may act as an interactor when genes can replicate differentially within organisms. At higher selection levels the interacting unit can be formed by cells, multicellular organisms, groups, or species.

Buss (1987) proposed and Maynard Smith and Szathmáry (1995) elaborated the hypothesis that the transitions to higher reproductive units are associated with transitions in the rules of natural selection. A comparable hypothesis was formulated by Michod (1999), who describes that transitions to higher-level reproductive units are likely to be induced by transitions to higher levels of selection. Transitions to higher levels of selection can induce transitions to higher reproductive units by promoting co-operative reproduction among lower-level units. Co-operative reproduction among lower-level units is typically fitness costly at that lower level, but co-operation may provide a fitness benefit at the next higher-level, and this benefit may outweigh the cost.

Although higher-level selection may outbalance lower-level costs of co-operation it has remained a relatively open question why selection at higher levels arises. In this paper I focus on the case of mobile organisms, where I show that selection by density-dependent competitive interactions can induce evolutionary transitions to higher-level selection, e.g., when there is selection for an increase in the energetic state of the organism. The hint is that the higher-level benefit of interactive advantage to interacting units with an increasing number of individuals is traded off against the lower-level cost of sharing the resource among the individuals of the interacting unit.

The major aim of my study, however, is to show that the transitions to higher-level selection by competitive interactions select for transitions in the co-operative reproduction among lower-level reproductive units, and that these transitions coincide with the major evolutionary transitions from asexual over pair-wise sexual to eusocial reproduction. I aim to shown that selection by density-dependent competitive interactions can equilibrate at four levels, and that these four equilibria coincide with respectively the asexually reproducing organism, the sexually reproducing pair, the co-operatively

reproducing unit, and the fully evolved eusocial colony. Hereby I propose the first theory of natural selection where a single ecological mechanism will explain four of the major life history transitions including the evolution and maintenance of sexual reproduction among reproductive units as diverse as sexual pairs and eusocial colonies.

In relation to the evolution of sexual reproduction I consider why interacting units with more than one individual tend to have sexual reproduction. I also consider why units with more than two individuals tend to have pair-wise sexual reproduction and sexually produced offspring workers. Alternative strategies include asexually produced offspring workers, and sexual reproduction at higher levels where there are plenty of sexual males that mate with the sexual female with all sexual individuals transferring a small fraction of their heritable code to the offspring.

My study is an extension of an earlier model (Witting 1997) that has been criticised for lack of clarity (Kricher 1998). Combined with other studies (Witting 1995, 1998, 2000a,b) this paper clarifies the original hypothesis by extending it and integrating it more firmly into the frameworks of evolutionary optimisation, evolutionary stable strategies, and multiple levels of selection. The fundamental selection mechanisms, however, remain basically the same between this study and the original model. The single major exception is sexual reproduction, where a differentiation between asexually and sexually produces offspring workers has been added to the original model in order to explain why sexual reproduction includes only a single male per female.

1.1 Three units of competition and co-operation

To describe the evolutionary transitions from asexual over pair-wise sexual to eusocial reproduction I deal with three units composed of individual organisms. Each unit represents a phenotypic trait, or dimension, where co-operation among the individuals of the unit can increase the interactive quality, or 'resource holding potential' (Parker 1974), of the unit at the highest inclusive level.

The first unit is the unit of selection given by the *interacting unit* 'that directly interacts as a cohesive whole with its environment in such a way that replication is differential' (Hull 1980, p. 318). This unit may exist at nearly all levels from genes and cells in multicellular organisms over individual organisms and groups of organisms to individual species or even groups of species. In the model developed in this paper the

interacting units are all below the population level at or above the level of the individual organism defining selection at levels from organisms to eusocial colonies. And the essential interactions that I use to define the level of selection are the density-dependent competitive interactions among these interacting units. At these levels the interacting unit is treated as an interactive trait where the larger and more co-operating units are selected to have a higher resource holding potential than the smaller and less co-operating units.

To allow the interacting units to evolve into sexually, co-operatively, and eusocially reproducing units I deal also with a *reproducing unit* and a *sexual unit*. In the proposed model the reproducing unit is defined as a sub-unit of the interacting unit, and the sexual unit is defined as a sub-unit of both the interacting and the reproducing units. Here the reproducing and sexual units are given by two different forms of co-operation among the individuals of the interacting unit, with the two forms of co-operation being traits that can enhance the resource holding potential of the interacting unit. More generally, however, interacting units may also be sub-units of both the reproducing and the sexual units, as is the case when cells multiply differentially within a multicellular organism. And the reproducing unit may also be a sub-unit of the sexual unit, as when sexual reproduction occurs between two otherwise independently reproducing hermaphrodites.

The reproducing unit is defined by a single replicating individual and from zero to infinite non-replicating individuals. The replicating individual is the individual that produces offspring and/or macrogametes and it is usually an asexually reproducing individual or a sexually reproducing female or hermaphrodite. The non-replicating individuals can be males that produce microgametes copying their heritable code to the offspring through the sexual reproduction of the female or the hermaphrodite. The non-replicating individuals may also be offspring workers that get their heritable code copied indirectly through the relatedness with the replicating and/or male individual/s. Independently of the specific composition of the reproducing unit, the individuals of the unit co-operate in copying their heritable codes into future generations, either through direct asexual or sexual reproduction or through indirect reproduction by inclusive fitness. As defined here, reproducing units with co-operative and eusocial reproduction are characterised by the presence of non-replicating individuals that reproduce indirectly through inclusive fitness. These units may thus be formed by both asexual and sexual organisms.

As the reproducing unit evolves as a sub-unit of the interacting unit the two units may or may not resemble one another. Whenever the interacting unit contains only a single individual the two units are identical, with both units being defined by the asexually reproducing organism. But when the interacting unit contains more than a single individual the two units may or may not resemble one another. In these cases it is only when the interacting unit contains a single replicating individual and the remaining individuals are non-replicating that the two units are similar. When instead the reproducing units are asexually reproducing organisms we have a case where all the individuals of the interacting unit are independent reproducing units. And at a more intermediate level we can have a case where the reproducing units are reproductive pairs and the interacting unit may resemble a colony of pair-wisely reproducing organisms.

In general we have that transitions to larger reproducing units can increase the interactive ability of the interacting unit. The energy and time that the non-replicating individuals save by not producing offspring or macrogametes can instead be allocated into interactive traits and competitive interactions. In this way the proportion of non-replicating individuals in the interacting unit and, thus, the size of the reproducing units can reflect interactive ability where, for interacting units of the same size, it is the unit with most non-replicating individuals and fewest reproducing units that has the highest resource holding potential.

The third dimension of co-operation is the sexual unit given by the individuals that join in sexual reproduction. The sexual unit is not present in asexual organisms. In sexual organisms the number of individuals in the sexual unit is usually one – a self-fertilising hermaphrodite – or two – a female and a male. But more generally there may be higher levels of sexual reproduction where females allocate heritable codes from more than a single male to the offspring. And sexually produced offspring need not necessarily obtain half of their genome from the mother and the other half from a single farther. To allow for the evolution of larger sexual units I apply a model where the sexual unit with three individuals is a unit with a single female and two males with each of the three individuals allocating one third of their heritable code to the offspring. And at the upper limit of sexuality the model allows for infinitely large sexual units composed of a single female and an infinite number of males with all individuals allocating an infinitely small fraction of their heritable code to the offspring.

As the sexual unit evolves as a sub-unit of both the interacting and the reproducing units the three units

may or may not resemble one another. The three units are identical when a sexually reproducing pair forms the interacting unit. When instead the interacting unit is a colony of co-operatively breeding birds, the three units differ with the reproducing units being defined by the co-operative groups within the colony, and the sexual units being defined by the sexual pairs within the co-operative groups. And when the interacting unit is an eusocial colony of termites we have a case where the interacting and the reproducing units are identical but where it is the sexual pair within the colony that forms the sexual unit.

The sexual unit may also enhance the interactive ability of the interacting unit. In populations with heritable variation we can expect genetic variants that differ in their interactive quality. And if the genetic variation in interactive quality is independent of the genetic variation in the level of sexual reproduction we expect that the average interactive quality of a sex level variant will be the same for all sex level variants. However, if there is assortative mating where the interactively superior males mate with the females that have the highest sexual level, the genetic variation in sexual reproduction may reflect the variation in interactive quality even though sexual reproduction does not enhance interactive quality in itself. And as argued below, for interacting units with non-replicating individuals, we may expect that a female with a larger than average level of sexual reproduction will use her sexual reproduction trait to replace some of her offspring workers with some of the most interactively superior males in the population. If this is the case, sexual reproduction will essentially play the role of an interactive trait by sorting the interactive quality variants over the sexual reproduction variants.

To see how such a sorting may occur let us consider a possible evolutionary transition from a population with asexually reproducing units to a population with sexually reproducing units. Assume that the reproducing unit contains both replicating and non-replicating individuals, and let initially reproduction occur asexually. But assume also that a replicating individual (female) has the ability to reproduce sexually, and that a non-replicating individual is an asexually produced offspring worker. As these offspring workers are genetically identical with their mother, they need not act as asexually or sexually reproducing individuals as long as they remain in the interacting unit with their mother. Here they may benefit more by acting as interacting individuals for the interacting unit and by letting their heritable code be copied indirectly through their relatedness with their mother.

In such populations we expect that there will be a sub-population of floating workers, i.e., offspring workers that have lost contact with their original interacting unit. Assume that at least a fraction of the non-replicating individuals are male-like individuals that cannot replicate, but that they have the ability to transfer genes to a replicating female that is willing to accept the genes and transmit at least some of them to her offspring. The floating males are thus reproductively dead unless they can find a replicating female and reproduce sexually. And when females are interested in enhancing the interactive quality of their interacting unit, we may expect selection for sexual selection where a female chooses floating males that are interactively superior to her offspring workers. We may also expect selection for sexual selection where the interactively superior males dominate the inferior males in order to have access to the females with the highest level of sexual reproduction, i.e., access to the females that allocate the largest fraction of the male genome to the offspring. If these forms of sexual selection evolve we can expect that the floating males will be distributed in such as way that the interactive quality of the males attracted to females is proportional to the fraction of the male genome that the female transfers to the offspring.

If the females with the highest level of sexual reproduction begin to enhance the interactive quality of the interacting unit by attracting the interactively superior males, we may also expect selection for sexually produced offspring workers at the cost of asexually produced offspring workers. This is because when the offspring workers are produced sexually instead of asexually it is more efficient for the female to enhance the interactive quality by attracting sexual males. With sexually produced offspring workers the inheritable component of the interactive quality of the male is transferred by sexual reproduction to the offspring workers. Thus, if a female can attract a male with a larger interactive quality than herself, she will gain fitness through interactive competition not only directly through the male, but also indirectly through the transmission of the male genome to her offspring workers. For the case with sexually produced reproducing offspring but asexually produced offspring workers the heritable component to the interactive quality of the offspring workers is given exclusively by the heritable code of the female being unaffected by the interactive quality of the male/s in the interacting unit. Hence, in this case, the female gains no extra interactive quality than that associated directly with the sexual males that she can attract.

There is also another important difference between the interactive quality gained through sexual reproduc-

tion for cases with asexually and sexually produced offspring workers. If, as it may be expected due to intra-population sorting of interactive males over sexually reproducing females, a given female attracts males of approximately the same interactive quality, then, for the case with asexually produced offspring workers, it follows that the interactive quality of sexual reproduction is proportional to the number of sexual males that engage in sexual reproduction with the female. This results from the simple fact that with asexually produced offspring workers the interactive quality of sexual reproduction is given exclusively by the quality of the sexual males and, thus, it is proportional to the number of males.

But with sexually produced offspring workers there is a diminishing return where the extra interactive quality that the female can gain by adding an extra male to her sexual unit is a declining function of the number of males in the unit. Initially, when the females goes from asexual to sexual reproduction by attracting the first sexual male, she gains more interactive quality than for the corresponding case with asexually produced offspring workers. This is because all her offspring workers inherit approximately half of the interactive quality of the male (if we assume that the interactive quality is randomly distributed over the genome). But when an additional male of approximately the same interactive quality is added at the cost of an offspring worker, the interactive quality gained directly from the replacement corresponds only to the quality of a half male. And the interactive quality gained in each of the remaining offspring workers correspond only to the interactive quality of 1/6 male. This is because the interactive quality to be gained is gained exclusively through the replacement of the female genome in the offspring workers. And as the genomic fraction that the offspring workers receive from the female is a declining function of the number of males in the sexual unit it follows that the interactive quality to be gained is a diminishing function of the number of sexual males per female. As shown later, the diminishing return with sexually produced offspring workers might be the essential factor that determines why sexual reproduction tends to involve only two individuals with the offspring receiving half of its genome from the mother and the other half from the father.

1.2 Costs of co-operation

The co-operation that defines the interacting, reproducing, and sexual units is typically costly to the individuals that form the units. For a sexually reproducing pair

the costs of the reproducing and sexual units resemble the well-known costs of sexual reproduction. Maynard Smith (1968, 1971, 1978) noted that sexual reproduction between a male and a female has a two-fold cost of the male, and Williams (1975, 1980, 1988) noted that it has a two-fold cost of meiosis. The two-fold cost of the male is the fact that asexual mutants increase twice as fast in numbers as sexuals when the asexual variant produces the same number of offspring as the sexual female. The two-fold cost of meiosis, on the other hand, is expressed in terms of genomic dilution where asexual mothers transmit all their genes to their offspring while sexual mothers transmit only half. It is usually said that sexual reproduction is two-fold costly, but sexual reproduction between a male and a female can be four-fold costly when the cost of the male is combined with the cost meiosis.

Not all sexual organisms experience the costs of sexual reproduction. Hermaphrodites evidently avoid the two-fold cost of the male, and they may also avoid the two-fold cost of meiosis. As hermaphrodites reproduce through both the female and the male function, they can resemble asexual self-replicators in the way that on average a gene gets one copy through to the next generation for each offspring produced by the hermaphrodite. Dioecious organisms may also reduce the costs of sex. If the species sometimes reproduces sexually and sometimes asexually both the cost of males and the cost of meiosis may be substantially reduced (Williams 1975; Maynard Smith 1978; Green and Noakes 1995).

The cost of the reproducing and the sexual unit do generally not resemble the two-fold cost of the male and the two-fold cost of meiosis. As defined in this paper, the cost of the reproducing unit is the cumulated cost of the non-replicating individuals in the reproducing unit, assuming that the replicating individuals produce the same number of offspring independently of the size of the reproducing unit. This cost can vary from zero to infinity dependent upon the number of non-replicating individuals per unit. The cost is zero when there is no non-replicating individuals, and it is the two-fold cost of the male when the reproducing unit is a sexual pair. The cost is three-fold in co-operatively breeding organisms where the sexual pair is associated with a single offspring, and the cost is infinity in eusocial species with an infinite number of offspring workers. For the case of this paper, where non-replicating individuals are assumed to be either offspring or sexual males, the cost of non-replicating individuals can be divided into the cost of males and the cost of non-reproducing offspring with both costs having the potential to vary between zero and infinity. The cost of males, for example, is larger

than two-fold when the sexual unit is larger than two and there is more than a single male per female.

Like the two-fold cost of the male is a special case of the cost of the reproducing unit, the two-fold cost of meiosis is a special case of the cost of the sexual unit. As defined in this paper, the cost of the sexual unit is the cost of dilution of the female's heritable code in the offspring and this cost may range from zero to infinity. The cost of dilution is close to zero when the heritable code of the offspring is provided almost entirely by the mother and only a tiny fraction is provided by a father. The cost is the two-fold cost of meiosis for the usual form of sexual reproduction, and it is three-fold when the sexual unit contains a female and two males and all three individuals transmit one third of their genome to the offspring. Likewise the cost of the sexual unit is infinity at the limit where the sexual unit contains a single female and an infinite number of males and all individuals transmit an infinitely small fraction of their genome to the offspring.

As defined in this paper the cost of the interacting unit is the cost of sharing local resources. When individuals aggregate into co-operating groups they will, relative to the situation with uniformly distributed individuals, exploit the resource locally in the immediate surroundings of the group. In an extreme case the amount of resource available for reproduction per interacting unit is the same independently of the number of individuals in the interacting unit. In this case the cost of the interactor is proportional to the number of individuals in the interacting unit, implying that the cost is two-fold for the case with two individuals in the unit. Thus, the cumulative cost may be six-fold for the case of sexual pair-wise reproduction.

1.3 Explaining reproductive modes

For natural organisms beyond the lowest level of reproduction we expect that the costs of the interacting, reproducing, and sexual units will be balanced by advantages provided by those units. It is thus essential to explain why the apparent benefit in mobile organisms of both the interacting and the reproducing unit is zero for asexual self-replicators, two-fold for pair-wise reproduction, three-fold for co-operative reproduction among three individuals, and close to infinity for eusocial reproduction. Likewise it is essential to explain why the apparent benefit of the sexual unit is zero for the asexual self-replicator, and why it is two-fold and only two-fold for dioecious sexual organisms independently of whether the organism reproduces pairwisely, co-operatively, or eusocially.

According to Kondrashov (1994) there has been at least 20 different attempts to explain advantages that can outbalance the cost of sexual reproduction (reviewed by Bulmer 1994; Ebert and Hamilton 1996; Hurst and Peck 1996). Nearly all of these models are reflections over the hypothesis that genetic diversity is beneficial to the organism *per se*. The various versions of the Fisher-Muller hypothesis suggest that sex and recombination protect against a genetic deterioration caused by the accumulation of deleterious mutations (e.g., Fisher 1930; Muller 1932, 1964; Manning and Thompson 1984; Wagner and Gabriel 1990; Charlesworth et al. 1993; Lynch et al. 1993, 1995; Peck 1994; Peck et al. 1997). Most of these studies provide only a long-term advantage to sexual populations, while they lack a short-term advantage that will explain the evolution of sexual reproduction and the maintenance of sexual reproduction for cases where asexual variants arise in sexual populations. Kondrashov's (1982) synergetic-fitness theory, however, can provide a short-term advantage given a special type of deleterious mutations that act together so that each gene becomes increasingly deleterious as the number of deleterious mutations increases. And Peck et al. (1999) show that the Fisher-Muller hypothesis may provide a short-term advantage if the population is subdivided into demes with sufficiently low migration among demes.

Another class of models is based on the idea that sexual reproduction may evolve because recombination produces genetically variable offspring (Weismann 1889), which may increase the speed and efficiency of natural selection (Kondrashov 1993; Barton 1995; Feldman et al. 1997). Genetically variable offspring may provide an advantage in biotic interactions (Bell 1982; Bell and Maynard Smith 1987), for example, in host-parasite interactions where sexual reproduction can stores genes that currently are bad but can protect against future mutant parasites (Hamilton 1980; Hamilton et al. 1990; Ebert and Hamilton 1996). Another example is the sib competition models of Williams (1975) and Young (1981) that assume that competition is more severe between asexual sibs, which are genetically identical, than between sexual sibs, which are genetically diverse. More recently it has been suggested that sexual reproduction may evolve or be evolutionarily maintained by non-random mating that accelerates the evolution of beneficial traits (Kodric-Brown and Brown 1987; Davis 1995; Jaffé 1996, 1999), or because of interactions among the different genetic models (West et al. 1999).

It has been said that none of the genetic hypotheses for the evolution of sexual reproduction are very

convincing (Green and Noakes 1995). The models will generally not explain why asexual reproduction in mobile organisms is more common in negligible sized organisms than in larger organisms. And nor will they explain why the sexual unit is a single male per female with the average offspring receiving half of the genes from the father and the other half from the mother. The genetical models tend to predict that only a small degree of sex is fine (Green and Noakes 1995; Hurst and Peck 1996; but see Peck and Waxman 2000), suggesting that the degree of gene exchange that occurs among haploid and asexually reproducing prokaryotes may be sufficient to account for most of the genetic diversity hypotheses. The pluralist approach of West et al. (1999) may provide a more efficient framework for generating an advantage that may outbalance the two-fold cost of meiosis. However, it might be more likely that the beautiful and simple phenomenon of sexual reproduction in higher organisms has evolved by a simple and clear-cut mechanism, instead of being explained by messy interactions among very different processes (Kondrashov 1999).

Reproducing units with more than two individuals have traditionally been explained by Hamiltonian models of inclusive fitness (Hamilton 1963, 1964), relabelled kin selection by Maynard Smith (1964). These models are essentially group selection models (Hamilton 1975; Sober and Wilson 1998) that aim at explaining why offspring choose to raise sibs instead of raising their own offspring. Assuming that the haplodiploid genome is more ancestral to hymenoptera than eusociality, Hamilton (1964) noted that hymenoptera can be predisposed to eusociality because of the high relatedness among sisters of haplodiploids. Trivers and Hare (1976) showed that sex allocation theory is central for this mechanism to work; haplodiploids are predisposed to eusociality only if the sex ratio of the sexual caste of the ancestor is female biased. Female biased sex ratios and, thus, the potential evolution of eusociality might arise through split sex ratios (Grafen 1986), where broods produced at different times (Seger 1983) or under different conditions (Frank and Crespi 1989) have different sex ratios. As co-operative and eusocial reproduction are widespread also in diploid species the high relatedness among sisters in haplodiploids may not be the factor that induces the evolution of eusocial colonies. And indeed it has been suggested that a haplodiploid genome may evolve from interactions among sexuals in eusocial species (Witting 1997).

Other factors than relatedness have also been proposed as the essential components that induce the evolution of eusocial colonies. Alexander (1974), Michener and Brothers (1974), and Stubblefield and Charnov (1986) argue that eusocial behaviour may evolve by parents that force their offspring to co-operate. Evans (1977) and Andersson (1984) that nest building may be the essential factor; and Jarvis et al. (1994) that mammalian eusociality may evolve by mutual benefit during ecological windows of opportunity.

In this paper I use multilevel selection by density-dependent competitive interactions to explain that the interacting, reproducing, and sexual units can outbalance zero cost at the lower limit of low-energy organisms with negligible body masses; that each of the three units can outbalance a two-fold cost for high-energy organisms with non-negligible body masses in evolutionary equilibrium; that the interacting and reproducing units can outbalance a three-fold cost, while the sexual unit can outbalance only a two-fold cost for high-energy organisms with body masses that increase exponentially at an evolutionary steady state; and that the interacting and reproducing units can outbalance up to infinite cost, while the sexual unit can outbalance only a two-fold cost for high-energy organisms with upward constrained body masses.

1.4 Long-term evolution by density-dependent selection

Traditional life history models (reviewed by e.g., Roff 1992; Stearns 1992; Bulmer 1994; Charlesworth 1994) tend to be based on a concept of short-term evolution, where some life history traits are predicted from local constraints like genetic covariance, phylogenetic constraints, and physiological trade-offs. The evolution of body mass is one example where large body masses have been predicted from a proportional relationship between the body mass and the rate of reproduction (McLaren 1966; Schoener 1969; Case 1979; Roff 1981, 1986; Lundberg and Persson 1993). Although the proportional relationship is confirmed empirically in many species (Peterson 1950; Robertson 1957; Wooton 1979; Roff 1982; Peters 1983; Reiss 1989) it was never explained from constraints that lie outside the domain of evolutionary biology, and it is likely that the relationship is the product of natural selection.

For the type of long-term evolution considered here it seems to be more appropriate to assume the complete absence of evolutionarily determined constraints. It is only when such local constraints are not included in the model that we can expect the predictions to be reflections of the global constraints that shape the process of long-term evolution. One difficulty with the long-term approach is to construct life history models where

the relationships among the different traits reflect only true constraints that cannot be altered by natural selection, i.e., constraints that are evolutionarily fixed because they arise from laws that lie outside the domain of evolutionary biology. A first attempt for such models was developed for mobile organisms by Witting (1997), who assumes that life history traits evolve independently of each other unless we have a non-biological law that clearly explains why the different traits should be linked to one another. As the interactions and covariance among traits in traditional models tend to be based on imperial evidence, instead of being deduced from first principles of non-biological laws, it follows that the long-term model developed here has considerably less trait covariance than a traditional model that would deal with the same traits. The more specific reasons for excluding some of the traditional covariance from my model is given in Section 2 under the subsections that deal with the specific traits.

But what may the global constraints that shape long-term evolution be? At the level intrinsic to the organism we may generally expect that they are reflections of physical laws, as is the case for energetic constraints. The intrinsic components of genetics and phylogeny, on the other hand, may only constrain short-term evolution because these components are products of natural selection and random events, and thus they are expected to be unstable at the longer timescale. At the level of ecological constraints extrinsic to the organism we also expect that most of the long-term constraints must arise from physical laws. But here there are important exceptions where long-term constraints arise from the origin of natural selection.

To see this note that natural selection has been define by the origin of self-replicators (Michod 1999; but see Lifson and Lifson 1999). These replicators are also referred to as exponential replicators because the self-replicating process generates an exponential increase in the abundance of self-replicating individuals. And in a limited world it follows that exponential increase induces competition among the individual self-replicators for the limited resources. Hence, through the process of density-dependent competition, the origin of self-replication defines the origin of density-regulated population growth and density-dependent selection.

Density regulation arises from exploitative and interactive (interference) competition, also referred to as respectively scramble and contest competition. I consider density regulation by exploitative competition to be the reduction in the per capita share of resource that occurs when the increasing population consumes an increasing amount of resource, assuming that all individuals have equal access to the resource and that there are no interactions among individuals. Regulation by interactive competition is considered to be the additional regulating component that arises from competitive interactions.

My analysis of interactive competition relates to the baseline case with pair-wise contests between randomly selected interacting units, with the rate of contests, i.e., the number competitive encounters per interacting unit per unit time, being positively related to population density. It is also assumed that the competitive game can be approximated by a population game where each variant is playing against the population average. And in my modelling I do not explicitly consider the behavioural games of competition. It is instead assumed that the payoff of interactive competition can be approximated by a log-linear function of the ratio between the trait value of a variant and the average trait value in the population, and that the slope of payoff differentiation is linearly related to the rate of contest competition. This intra-population differentiation in the payoff reflects the fact that interactive competition causes a density-dependent bias in resource access in favour the interacting units that have the highest interactive quality, i.e., in favour of the units with the highest resource holding potential.

Classical models of density-dependent selection arose from the concept of r- and k-selection (reviewed by Mueller 1997). The basic idea was considered by Fisher (1930), but the concept was proposed formally by MacArthur (1962) and MacArthur and Wilson (1967) and developed theoretically by others (e.g., Anderson 1971; Charlesworth 1971, 1994; Roughgarden 1971; Clarke 1972). The mechanism of r- and k-selection operates through an increase in the intrinsic growth rate, and this has been seen as a reflection of Fisher's (1930) Fundamental Theorem of Natural Selection (Witting 2000a). The original concept is based on the assumption that the relative fitnesses at a specific population density are constant, which is inappropriate whenever competitive interactions play an essential role in density regulation. For cases with density-dependent competitive interactions the intrinsic growth rate may decline (Witting 2000a), and we need to apply the game theoretical concepts of Evolutionary Stable Strategies (Maynard Smith and Price 1973; Maynard Smith 1982; see also Vincent and Brown 1988; Vega-Redondo 1996; Dugatkin and Reeve 1998; Hofbauer and Sigmund 1998) and Continuously Stable Strategies (Eshel and Motro 1981; Eshel 1983; see also Taylor 1989; Christiansen 1991; Metz et al. 1992, 1996; Dieckmann 1997; Eshel et al. 1997; Geritz et al. 1997, 1998; Kisdi 1999).

The game theoretical concept of Continuously Stable Strategies (CSSs) is rather promising for the type of long-term evolution considered in this paper. Although the CSS is a genetic-free concept it has been shown that the long-term convergence to such strategies is independent of the genetic structure for a wide range of genetic assumptions (Eshel and Feldman 1984; Liberman 1988; Matessi and Di Pasquale 1996; Eshel et al. 1997; Eshel et al. 1998). For the case of an one-dimensional continuity of pure strategies the long-term convergence to a CSS is deterministic and virtually independent of the distribution of mutations (Eshel et al. 1997). For multi-dimensional strategies, as considered in this paper, the long-term convergence and stability may depend on genetics (Matessi and Eshel 1992; Matessi and Di Pasquale 1996). Loose linkage may prevent two traits from reaching their fitness optimum when they are related to one another by a trade-off and the fitness function is everywhere increasing with respect to both traits (Matessi and Di Pasquale 1996). In this case all points on the trade-off boundary can be Evolutionary Stable Strategies even though there is only a single point that defines the fitness maximum. However, in this instance we might expect selection for an increase in the linkage between the two traits. And with absolute linkage long-term evolution will converge towards the fitness optimum (Matessi and Di Pasquale 1996). More generally, for multi-dimensional strategies and selection on all possible genetic structures it remains to be shown if genetic constraints can prevent a long-term convergence toward the optima of genetic free selection.

2 The model

2.1 Levels of reproduction

To explain the evolutionary transitions from asexual over sexual to eusocial reproduction I assume a particular nesting of the interacting, reproducing, and sexual units. I let the interacting unit take the highest inclusive level where it contains both the reproducing and the sexual units, and I let the sexual unit be a sub-unit of the reproducing unit. This structure is used as a general model for mobile organisms, but I also consider two cases where the interacting unit is not at the highest level. The first is considered in the discussion in this paper, and it is the case where the interacting unit is at the individual level being contained both within the reproducing and within the sexual unit. I argue that this case is likely to be a general model for sexual reproduction in sessile organisms. The second case is

N	Population density
ι	Level of competitive interactions among interacting units
γ_α	Density regulation by exploitation
γ_ι	Density dependence in number of competitive interactions
μ	Cost, or payoff, of competitive interactions
ψ	Within population slope in μ
γ	Total density regulation, $\gamma = \gamma_\alpha + \mu\gamma_\iota$
λ	Discrete Malthusian parameter
r	Malthusian parameter
R	Lifetime reproduction
p	Survival scalar
ϵ	Energetic state; the energy available for replication
ϵ_φ	Energy used for traits of non-replication
w	Body mass
z	Tightness & co-operation of individuals in interacting units
n	Number of individuals per interacting unit
n_θ	Number of reproducing units per interacting unit and number of replicating individuals per interacting unit
n_φ	Number of non-replicating individuals per interacting unit, $n_\varphi = n_\phi + n_\omega$
n_ϕ	Number of sexually reproducing males per interacting unit
n_ω	Number of offspring workers per interacting unit
φ	Proportion of non-replicating individuals, $\varphi = n_\varphi/n$
ϕ	Proportion of males among sexual individuals, $\phi = n_\phi/(n_\phi + n_\theta)$, and the fraction of the offspring's genome that comes from the father/s
d	Number of spatial dimensions in which the organism forages

Table 1: Important symbols.

when the interacting unit of a eusocial species with a sexual unit of two individuals does not contain the sexual male. As shown by Witting (1997), the exclusion of the sexual male from the interacting unit may explain the transitions in ploidy levels and worker sex ratios from eusocial termites to eusocial hymenoptera.

The four reproductive levels to be deduce from first principles of density-dependent competitive interactions are given by the phenotypic states $\mathbf{P}^{*i}$, $\mathbf{P}^{**}$, $\mathbf{P}^{*s}$, and $\mathbf{P}^{*c}$ in Table 2, with symbols explained in Table 1. The phenotypic state $\mathbf{P}^{*i}$ is the asexual self-replicator with a single individual in the interacting and the reproducing units. This organism has a negligible body mass, a haploid genome, no sexual unit, no males, and no offspring workers. Relative to $\mathbf{P}^{*i}$ the three phenotypic states $\mathbf{P}^{**}$, $\mathbf{P}^{*s}$, and $\mathbf{P}^{*c}$ are sexual organisms with relatively large body masses. These organisms

have sexual units of one female and one male, offspring that receive half of the heritable code from each parent, and a diploid genome given parallel inheritance where all parents transmit homologous copies of the heritable code to the offspring. The differences between the three phenotypic states $\mathbf{P}^{**}$, $\mathbf{P}^{*s}$, and $\mathbf{P}^{*c}$ lie in the interacting unit where the number of individuals are 2, 3, and ∞ respectively, and in the reproducing unit where the corresponding number of sexually produced offspring workers are 0, 1, and ∞.

2.2 Basic model

Selection in the initial self-replicator $\mathbf{P}^{*i}$ lies at the limit of prebiotic selection. It is a general view that prebiotic selection is given not by exponential replication, but by a more general form of replication

$$d\tilde{N}/dt = k\tilde{N}^\beta \qquad (1)$$

where $\tilde{N}$ is the replicator abundance, k a constant, and β the order of the replication process given, e.g., by the number of replicators it takes to produce a new replicator (Michod 1983; Szathmáry and Maynard Smith 1997; Lifson and Lifson 1999). Parabolic replication with $\beta < 1$ has been observed in enzyme-free template replication of RNA-like strands (Kiedrowski 1986; Zielinski and Orgel 1987; Sivers and Kiedrowski 1998), while hyperbolic replication with $\beta > 1$ is the replication process for hypercyclic replicators. True self-replicators, however, with $\beta = 1$ are exponential replicators with Malthusian growth (Malthus 1798), and self-replication has been considered to define the origin of natural selection (Michod 1999; but see Lifson and Lifson 1999).

It is the selection that arises from the replication process of true self-replicators that is considered in this paper. With self-replication and density regulation we have that

$$\tilde{N}_{t+1} = \tilde{N}_t \lambda_m f(\tilde{N}_t) \qquad (2)$$

$\mathbf{P}$	w	n	n_θ	n_φ	n_ϕ	n_ω	ϕ
$\mathbf{P}^{*i}$	≈ 0	1	1	0	0	0	1
$\mathbf{P}^{**}$	$\gg 0$	2	1	1	1	0	1/2
$\mathbf{P}^{*s}$	$\gg 0$	3	1	2	1	1	1/2
$\mathbf{P}^{*c}$	$\gg 0$	∞	1	∞	1	∞	1/2

Table 2: The four phenotypic states ($\mathbf{P}$) of the study. $\mathbf{P}^{*i}$ is the asexual self-replicator, and $\mathbf{P}^{**}$, $\mathbf{P}^{*s}$, and $\mathbf{P}^{*c}$ are higher eukaryotic-like organisms with respectively pair-wise, co-operative, and eusocial reproduction. Symbols are explained in Table 1.

where λ is the discrete Malthusian parameter, subscript m denotes its maximum, and $f(\tilde{N})$ is a density regulation function that declines monotonically from one to zero as the abundance increases from one to infinity (assuming no Allee effect). Instead of representing density regulation by the general model of eqn 2 let me, for the case of simplification, focus on the process that is linear at the logarithmic scale of population dynamics. The density regulation function can then be defined as

$$f(\tilde{N}) = \begin{cases} \nu \tilde{N}^{-\gamma} & \text{if } \tilde{N} \geq \dot{\tilde{N}} \\ 1 & \text{if } \tilde{N} < \dot{\tilde{N}} \end{cases} \qquad (3)$$

where $\dot{\tilde{N}} = 1$ is the abundance where the effects of density regulation vanish, γ is the curvature of the density regulation function, and $\nu = \dot{\tilde{N}}^\gamma$. Thus, in relation to the Malthusian parameter $r = \ln \lambda$ the density regulation function is

$$r = r_m - \gamma \ln N \qquad (4)$$

where $r_m = \ln \lambda_m$ is the maximal growth rate and $N = \tilde{N} \nu^{-1/\gamma}$. The assumption of linearity will only have a minor influence on the results. This is because the essential results depend, not on the absolute value of the density regulation process, but on the intra-population slope in the density regulation process around the population dynamic equilibrium.

Let the density regulation parameter γ be partitioned into two components that reflect respectively exploitative and interactive competition, i.e., let $\gamma = \gamma_\alpha + \mu \gamma_\iota$, where subscript α indicates exploitative competition, subscript ι indicates the level of interactive competition, and μ is the cost, or payoff, per competitive interaction. Then let

$$r = r_m - \gamma_\alpha \ln N - \mu \iota \qquad (5)$$

where

$$\iota = \gamma_\iota \ln(N/n) \qquad (6)$$

is the level of interactive competition that reflects the number of competitive encounters per interacting unit per unit time, with n being the number of individuals per interacting unit. As a competitive encounter takes some time, the defined density dependence of ι has a realistic convex shape, while at the same time it ensures logarithmic linearity in relation to the density regulation function of eqn 3. For a general discussion on density-dependent encounter probabilities see Nakajima (2001). Given eqns 5 and 6, the density regulation function of eqn 3 for $\tilde{N} \geq \dot{\tilde{N}}$ is $f(N) = n^{\mu \gamma_\iota} N^{-\gamma}$. Thus,

in discrete time at the population dynamic equilibrium, eqn 5 becomes

$$\lambda^* = \lambda_m n^{\mu\gamma_\iota} N^{*-\gamma} = 1 \qquad (7)$$

with $N^* = \sqrt[\gamma]{\lambda_m n^{\mu\gamma_\iota}}$, superscript $*$ denoting population dynamic equilibrium, and $\lambda^* = e^{r^*}$.

For the case with age-structure it is shown in the Appendix that the discrete growth rate at the population dynamic equilibrium is $\lambda^* = pR^*$, where $p = R_0^*/R^*$ is a survival scalar, with R_0^* being net lifetime reproduction and R^* lifetime reproduction at equilibrium. And from the energetic constraints intrinsic to the organism we may expect that the relationship between lifetime reproduction and body mass w is

$$R^* = \epsilon^*/w \qquad (8)$$

where $\epsilon^* = \epsilon/\lambda_m$ is the energetic state of the organism, being defined as the attainable resource available for lifetime reproduction at population dynamic equilibrium, and ϵ is the corresponding state for the case of unexploited resources and no interactive competition. The trade-off of eqn 8 is expected because with ϵ^* amounts of energy allocated to reproduction ϵ^*/w offspring can be produced so that the organism can choose to allocate resources either to the body mass w or to the rate of reproduction R. The inverse relationship of eqn 8, however, holds only when the offspring are reared by the parents. But not only is this case reflected in many species of higher animals; it is also the expectation for simple self-replicators that reproduce by binary fission. Thus, it may be argued that the energetic trade-off reflects a basic reproductive constraint from which other reproductive modes have evolved.

The life history constraint of eqn 8 differs somewhat from those of traditional life history models. Usually it is assumed that the reproductive rate R is approximately proportional to body mass (e.g., McLaren 1966; Roff 1981, 1986; Gerritsen 1984; Stearns and Koella 1986; Lundberg and Persson 1993) which, for eqn 8, is the case if the energy available for reproduction scales to the second power of body mass, i.e., if $\epsilon \propto w^2$. However, as there seems to be no general non-biological law to explain this relationship I follow the independence principle of long-term evolution assuming evolutionary independence between ϵ and w.

In my study I also assume that the survival probability p is independent of body mass, which is also in contrast to more traditional life history models. At the within-population scale in nature the survival rate is often observed to increase with body mass (McGurk 1986). Nevertheless, the assumption in traditional life history models has been that the survival probability declines with body mass because larger individuals tend to reproduce at a later age. However, at larger evolutionary scales, as revelled by between species comparisons, the probability of survival to reproductive age seems to be independent of body mass [Fig. 1 in Witting (1995)]. Also, from the age-structured model in the Appendix it follows that p is expected to be independent of life span and absolute reproduction (see Witting 1997) suggesting that p is invariant among organisms with similar bauplans. Thus, in the absence of a clear and general constraint relating body mass to the survival scalar p, I follow the principle of long-term evolution assuming independence between p and w.

2.3   Interacting unit

To extend the life history model of eqn 8, let the interacting unit be a group of n individuals that co-operate in the defence of resource items, and let $0 \leq z \leq 1$ be the tightness of the group. Let $z = 0$ be the limit where there is no co-operation and individuals are uniformly distributed on the resource, and $z = 1$ the limit with complete co-operation and individuals that are aggregated into tight groups of n individuals.

When individuals aggregate into groups they will, relative to the situation with uniformly distributed individuals, exploit the resource locally in the immediate surroundings of the group. Given no interactive competition, let the limit $z = 1$ correspond to groups that are so tight that a group of n individuals has the same amount of resource available for reproduction as a single individual when individuals are uniformly distributed. Thus, the amount of resource that is available for an interacting unit of tightness $z = 1$ is $\epsilon^* = n\epsilon^*(1-k)$, where k is the cost of group formation. By rearranging this equation we find that $k = (n-1)/n$ and, thus, $\epsilon^*[1 - (n-1)/n]$ is the average amount of resource that an individual has available for reproduction in an interacting unit with n individuals and tightness $z = 1$. More generally the energy that an individual has available for reproduction in interacting units of arbitrary tightness and size is $\epsilon^*[1 - (n-1)z/n]$. Thus, extending from $\lambda^* = pR^*$ and eqn 8, the per generation growth rate is

$$\lambda^* = p\epsilon^*[1 - (n-1)z/n]/w \qquad (9)$$

For eqn 9 it follows that pair formation is two-fold costly in terms of population dynamic growth, i.e., that $\lambda_{n=1}/\lambda_{n=2} = 2$, where $\lambda_{n=1}$ and $\lambda_{n=2}$ are respectively the growth rates of a single individual ($n = 1$) and a tight group with two individuals ($n = 2$).

In eqn 9 it is implicitly assumed that groups of individuals can evolve to be so tight that they are no better in exploiting the resource than a single individual in the absence of group formation. More generally, however, we may expect that this is not always the case. Nevertheless, I focus on the simple model because it represents the most difficult case where group formation is least expected because the cost of group formation is at its highest. The more general case, with a variable cost of group formation, was analysed by Witting (1997), who illustrated that a lower cost may stimulate the evolution of several reproducing units within a single interacting unit.

2.4 Reproducing unit

Let, for the case with fully evolved reproducing units, an interacting unit of n individuals be formed by $1 \leq n_\theta \leq n$ reproducing units, and assume that all the reproducing units in the interacting unit have the same number of individuals n/n_θ. Let the reproducing unit/s contain a single and only a single replicating individual, like an asexually reproducing individual or a sexually reproducing female. Let the rest of the individuals in a reproducing unit be non-replicating individuals that get their heritable codes copied into future generations by the help of the replicating individual. In this paper non-replicating individuals are either males that reproduce sexually with a female replicating individual, or offspring of the replicating individual that get their heritable code copied indirectly through their relatedness with the replicating individual, and their relatedness with the sexual male/s if sexual reproduction occurs.

To allow the number of reproducing units n_θ to evolve below n, define a non-replicating individual as an individual that uses the energy $\epsilon^*[1 - (n-1)z/n]$ for other purposes than replication, and let $0 \leq \epsilon_\varphi \leq 1$ be the fraction of the energy $\epsilon^*[1 - (n-1)z/n]$ that a potentially non-replicating individual uses for other purposes than replication. The individual is thus non-replicating when $\epsilon_\varphi = 1$, while it is fully replicating when $\epsilon_\varphi = 0$. Let $n_\varphi = n - n_\theta$ be the number of potentially non-replicating individuals per interacting unit, and let $\varphi = n_\varphi/n$ be the fraction of non-replicating individuals. The average amount of energy that is available for reproduction per individual is then $\epsilon^*[1 - \epsilon_\varphi \varphi][1 - (n-1)z/n]$ and the per generation growth rate is

$$\lambda^* = p\epsilon^*[1 - \epsilon_\varphi \varphi][1 - (n-1)z/n]/w \qquad (10)$$

As $\lambda_{\varphi=0}/\lambda_{\varphi=1/2} = 2$ by eqn 10 it follows that a non-replicating individual in interacting units of two individuals is two-fold costly ($\lambda_{\varphi=0}$ and $\lambda_{\varphi=1/2}$ are the growth rates for $\varphi = 0$ and $\varphi = 1/2$ respectively, given that $\epsilon_\varphi = 1$).

By eqn 10 it is assumed that non-replicating individuals do not allocate resources directly into the production of offspring. This is known not to be the case in many species; both males and offspring workers are often seen gathering resources for reproduction. Nevertheless, the simple model is maintained here. By focussing on the situation where non-replicating individuals do not help in the production of offspring I deal with the case where the cost of non-replicating individuals is largest and, thus, where their evolution by natural selection is most difficult to explain. And although the resource allocation of non-replicating individuals may not be directly comparable between the model and particular species, the mechanisms of the proposed model may still be responsible for the evolution of non-replicating individuals. For example, if the selection pressure of density-dependent competitive interactions will explain the evolution of non-replicating individuals when the cost of non-replication is largest, then secondarily after the evolution of non-replication the non-replicating individuals might be selected to dedicate at least some time and energy to the production of offspring.

2.5 Sexual unit

Let the evolutionary division of the n_φ non-replicating individuals into n_ϕ sexually reproducing males and $n_\omega = n_\varphi - n_\phi$ non-reproducing offspring workers define the evolution of the sexual unit. The individuals of the interacting unit is then

$$n = n_\theta + n_\phi + n_\omega \qquad (11)$$

where n_θ is the number of replicating individuals. The offspring workers n_ω may be produced either by asexual reproduction in the replicating individual or by sexual reproduction between the replicating female and the sexual male/s of the reproducing unit. From eqn 11 we find that the proportion of males among the sexually reproducing individuals is

$$\phi = n_\phi/(n_\phi + n_\theta) \qquad (12)$$

Allow for sexual and reproducing units that have only a fraction of a male associated with them. This situation will arise when a male is connected to more than a single reproducing unit dividing his time equally among units. Assume also that the fractions of the heritable code that the sexually produced offspring receives from the different parents are weighted according to the time

that each parent allocates to the sexual unit. Hence, the male fraction ϕ of eqn 12 is identical to the fraction of the genome that the offspring receives from (all) the father(s), and the female fraction $1 - \phi$ is identical to the fraction of the genome that the offspring receives from the mother. This implies that $\phi = 0$ represents asexual reproduction with the offspring receiving all its genes from the mother, and that $\phi = 1/2$ corresponds to the usual form of sexual reproduction where the offspring receives half of its genes from the mother and the other half from the father. The limit $\phi \to 1$, on the other hand, corresponds to the unusual form of sexual reproduction where there is infinitely many males per female and nearly all the genes in the offspring are inherited from the fathers. The widespread solutions to ϕ in natural populations include the haploid genome for $\phi = 0$, and the diploid or haplodiploid genome with meiosis and haploid gametes for $\phi = 1/2$.

When the reproducing units of eqn 11 have more than one individual but no males they correspond to clonal units. Note also that the degree of kin selection is positively related to the fraction of the non-replicating individuals that are offspring workers. At the limit where all non-replicating individuals are sexual males kin selection is absent, while it is fully developed when all the non-replicating individuals are offspring workers. Thus, when we determine the evolutionary optimum to the number of non-reproducing offspring per interacting unit we determine also the degree to which kin selection evolves.

Based on eqn 12, the per generation growth rate is

$$\lambda^* = p\epsilon^*[1 - \phi][1 - \epsilon_\varphi \varphi][1 - (n-1)z/n]/w \quad (13)$$

when given in terms of replica of the females genome. From eqn 13 it follows that $\lambda_{\phi=0}/\lambda_{\phi=1/2} = 2$. In relation to the widespread form of sexual reproduction this implies that the meiotic division of the diploid genome into haploid gametes is two-fold costly. Note also that the costs of the interacting, reproducing, and sexual units are additive. The two-fold cost of the male and the two-fold cost of meiosis adds up to a four-fold cost, i.e., $\lambda_{\varphi=0,\phi=0}/\lambda_{\varphi=1/2,\phi=1/2} = 4$, given that $n_\phi = n_\varphi$. And the cumulative cost is six-fold for pair-wise sexual reproduction between a female and a male, i.e., $\lambda_{n=1,\varphi=0,\phi=0}/\lambda_{n=2,\varphi=1/2,\phi=1/2} = 6$.

2.6 Selection by competitive interactions

All the traits $\mathbf{C} = \{\phi, \epsilon_\varphi, \varphi, n, n_\phi, z, w\}$ can be selected to enhance the interactive quality of the interacting unit. Individuals with a larger body mass (w)

can generally be selected to dominate smaller individuals. Larger (n) and more co-operating (z) units can be selected to dominate smaller and less co-operating units. Units with a higher fraction (φ) of more fully developed (ϵ_φ) non-replicating individuals can allocate more energy and time into competitive interactions than units with a lower fraction of less fully developed non-replicating individuals. And units with a higher level of sexual reproduction (ϕ & n_ϕ) can be selected to dominate units with a lower level of sexual reproduction.

As discussed in Section 1.1, we may expect the genetic male variants to be distributed over the genetic female variants in such a way that the interactive quality of the male/s and the number of males per interacting unit are proportional to the sexual level of the female. But how can we expect the interactive quality of sexual reproduction to depend on the number of sexual males per interacting unit? To describe this let the interactive quality of sexual reproduction be s_ϕ, and let it be given in a unit that reflects the difference in interactive quality between the sexually reproducing male and an asexually produced offspring worker. Then, for the case of asexually produced offspring workers, where workers do not inherit interactive quality from males, the interactive quality of sexual reproduction is proportional to the number of sexual males in the interacting unit

$$s_\phi \propto n_\phi \quad (14)$$

With sexually produced offspring workers we expect the workers to inherit some of the male's interactive quality. Hence, with sexually produced offspring workers the interactive quality of sexual reproduction is proportional to the number of sexual males, plus the number of sexually produced offspring workers multiplied by the difference Δs_w in interactive quality between a sexually produced offspring worker and an asexually produced offspring worker. That is, $s_\phi \propto n_\phi + n_w \Delta s_w$. And with sexual reproduction between a female and n_ϕ/n_θ males the fathers fraction of the offspring's genome is $n_\phi/(n_\phi + n_\theta)$. Thus, if the loci that codes for the interactive quality are distributed randomly over the genome, for the case of additive genetic variation, we can expect the difference in interactive quality between a sexually produced offspring worker and an asexually produced offspring worker to be

$$\Delta s_w \propto \frac{n_\phi}{n_\phi + n_\theta} \quad (15)$$

And with n_ϕ males and $n_\omega = n - n_\phi - n_\theta$ sexually produced offspring workers we find that the interactive

quality of sexual reproduction is

$$s_\phi \quad \propto \quad \frac{(n - n_\phi - n_\theta)n_\phi}{n_\phi + n_\theta} + n_\phi \qquad (16)$$
$$\propto \quad \frac{nn_\phi}{n_\phi + n_\theta}$$

Hence, when, for the case with sexually produced offspring workers, the number of sexually reproducing males n_ϕ increases from zero to $n - n_\theta$ there is a diminishing return to the interactive quality of sexual reproduction. And as $\phi = n_\phi/(n_\phi + n_\theta)$, we find that eqn 16 reduces to

$$s_\phi \propto n\phi \qquad (17)$$

Thus, the set of interactive traits is better described as $\mathbf{C} = \{\epsilon_\varphi, \varphi, n, s_\phi, z, w\}$, with $s_\phi = n_\phi$ for the case of asexually produced offspring workers and $s_\phi = n\phi$ for the alternative case of sexually produced offspring workers.

When competitive interactions and other forms of frequency dependency are absent the fitness profile $r^* = \ln \lambda^*$ is obtained directly from eqn 13

$$r^* = \ln\left(p\epsilon^*[1 - \phi][1 - \epsilon_\varphi\varphi][1 - (n-1)z/n]/w\right) \quad (18)$$

Relative to eqn 18 the fitness profile for the case with competitive interactions is biased in favour of the interactively superior interacting units. This fitness bias arises from the payoff of interactive competition (μ) where the interactively inferior units have a higher payoff than the interactively superior units. To describe this let μ be the average payoff associated with a competitive encounter for the average variant in the population, and let

$$\mu_i = \mu + \Delta\mu_i \qquad (19)$$

be the average payoff for the ith variant, with $\Delta\mu_i = \mu_i - \mu$ being the difference in payoff between the ith and the average variant. Let the payoff of interactive competition be a linear function of ln interactive quality so that, for any trait $c \in \mathbf{C}$,

$$\Delta\mu_i = \psi_c(\ln c - \ln c_i) \qquad (20)$$

where ψ_c describes the within population slope between the payoff of interactive competition and ln interactive quality of the trait c.

When the competitive game is the same for all traits $c \in \mathbf{C}$ we have a symmetrical case where $\psi_c = \psi$ for all $c \in \mathbf{C}$. Symmetry is quite widespread in evolutionary ecology (Charnov 1993), and similar competitive games may be expected when i) the intra-trait relationship between interactive quality and the value of a

trait is similar for all traits, and ii) all traits are used equally frequent in competition for the same type of resources. As the present model relates to competition for energetic resources, and as all the interactive traits considered can be crucial in determining the outcome of a competitive interaction we may generally expect that condition ii for similar competitive games is fulfilled. And as the relative interactive quality of a traits variant in the population is likely to reflect some general function of the ratio of that trait variant to the average trait in the population, condition i may also be generally fulfilled. It may thus be argued that symmetry ($\psi_i = \psi_j$) represents a baseline case, while cases of asymmetry ($\psi_i \neq \psi_j$) should be considered as more special cases.

From eqns 5, 19, and 20 the fitness of the ith variant is

$$r_i = r_m - \gamma_\alpha \ln N - [\mu + \psi_c(\ln c - \ln c_i)]\iota \qquad (21)$$

and, by eqn 18, the fitness profile for all traits $c \in \mathbf{C}$ at population dynamic equilibrium is

$$r_i^* = \ln\left(p\epsilon^*[1 - \phi_i][1 - \epsilon_{\varphi_i}\varphi_i][1 - (n_i - 1)z_i/n_i]/w_i\right)$$
$$+ \sum_{c \in \mathbf{C}} \psi_c\iota^*(\ln c_i - \ln c) \qquad (22)$$

where $\epsilon^* = \epsilon N^{*-\gamma_\alpha}e^{-\mu\iota^*}$. This profile reduces to eqn 18 when $\iota^* = 0$.

By eqn 22 the fitness profile for an interactive trait c is a two-dimensional function

$$r_i^* = f(c, c_i) \qquad (23)$$

where the fitness of the ith variant depends both on the trait value of that variant (c_i) and on the average trait value in the population (c). The selection gradient is then

$$\left.\frac{\partial r_i^*}{\partial c_i}\right|_{c_i=c} = \left.\frac{\partial f}{\partial c_i}\right|_{c_i=c} \qquad (24)$$

with $|_{c_i=c}$ indicating that the partial derivative is to be taken at the limit $c_i = c$. An evolutionary equilibrium c^{**} is where the selection gradient is zero ($\partial r_i^*/\partial c_i|_{c_i=c} = 0$). The equilibrium is an Evolutionary Stable Strategy (ESS) if

$$\left.\frac{\partial^2 r_i^*}{\partial c_i^2}\right|_{c_i=c=c^{**}} < 0 \qquad (25)$$

(Maynard Smith 1982), and an evolutionarily unstable branching point if $\partial^2 r_i^*/\partial c_i^2|_{c_i=c=c^{**}} > 0$ (Metz et al. 1996; Geritz et al. 1997, 1998; Eshel et al. 1997). The ESS may not be an evolutionary attractor. The ESS is

a convergent stable attractor, also known as a Continuously Stable Strategy (CSS), when

$$\frac{\partial}{\partial c}\left(\left.\frac{\partial r_i^*}{\partial c_i}\right|_{c_i=c}\right)\Bigg|_{c=c^{**}} < 0 \qquad (26)$$

while it is an evolutionary repellor when $\frac{\partial(\partial r_i^*/\partial c_i|_{c_i=c})}{\partial c|_{c=c^{**}}} > 0$ (Eshel 1983; Taylor 1989; Christiansen 1991). For the more simple case of eqn 18 the fitness profile is a one-dimensional function of the trait: $r^* = f(c)$. The selection gradient is then $\partial r^*/\partial c$, and the evolutionary equilibrium ($\partial r^*/\partial c = 0$) is an evolutionarily stable attractor when $\partial^2 r^*/\partial c^2|_{c=c^{**}} < 0$, and an evolutionarily unstable repellor when $\partial^2 r^*/\partial c^2|_{c=c^{**}} > 0$.

3 Results

3.1 Four evolutionary states

By eqns 6 and 7 the level of interactive competition at the population dynamic equilibrium is a function of the equilibrium density, while the equilibrium density is a function of the population dynamic growth rate. Thus, the level of interactive competition will depend on the evolutionary determinants of the life history traits in eqn 13, because it is these traits that determine the intrinsic component of the population dynamic growth rate. From eqn 13 we note that body mass is the only trait that can equilibrate the population dynamic growth rate within the complete range of $0 < \lambda_m < \infty$. We may thus expect that the body mass can act as an evolutionary buffer that will determine the level of interactive competition in the population.

This is supported by the evolutionary equilibrium in body mass. From eqn 22 the selection gradient on body mass is

$$\left.\frac{\partial r_i^*}{\partial \ln w_i}\right|_{w_i=w} = \psi_w \iota - 1 \qquad (27)$$

Then, as the within population slope ψ_w between the payoff of competitive interactions and $\ln w$ can be considered to be determined by ecological constraints, we may expect that the evolutionary equilibration of body mass operates through an evolutionary adjustment of the level of interactive competition so that

$$\iota^{**} = 1/\psi_w \qquad (28)$$

at the evolutionary equilibrium ($**$). This equilibrium can be shown to be a neutrally stable attractor (Witting, unpublished). The level of interactive competition at the evolutionary equilibrium in body mass is thus independent of the body mass at evolutionary equilibrium. This is unlike the equilibria of the other traits (Sections 3.2 to 3.4) where the equilibria are defined by relationships between the level of interactive competition and the average trait value in the population. Hence, given sufficient time, we can expect an overall equilibrium where the level of interactive competition is adjusted according to a body mass in evolutionary equilibrium, and where the other traits are adjusted so that their equilibrium values correspond with the competitive level determined by the body mass.

The evolutionary equilibrium in body mass, however, is based on a few implicit assumptions. The first is that the energetic state of the organisms is so high that the population dynamic growth can generate interactive competition at levels at or beyond $1/\psi_w$. For organisms at the lowest energetic state ($\epsilon \approx 0$) this is not necessarily the case. Even when the body mass is negligible, being situated at the lowest possible limit, these organisms may have so little energy available that the reproductive rate cannot generate the required growth in population density. Thus, we may expect that organisms at the lowest energetic level will have approximately zero interactive competition in the population, i.e., that $\iota = 0$. And then by eqn 27, we find that $\partial r_i^*/\partial \ln w_i|_{w_i=w} = -1$, which implies that low-energy organisms are expected to have negligible body masses that are situated at a lower limit.

Not only is the evolutionary equilibrium in body mass based on the assumption of a high-energy organisms ($\epsilon \gg 0$), but it is also based on the assumption that the energetic state is evolutionary stable, i.e., that $d\epsilon/dt = 0$. The latter assumption was relaxed by Witting (1997) who found that when the energetic state is allowed to evolve freed from evolutionary constraints, then, we can expect that the evolutionary process will equilibrate at an evolutionary steady state with an exponential increase in both the energetic state and body mass. At the evolutionary steady state the level of interactive competition was predicted to be $\iota = (4d-1)/(2d-1)\psi_w$, where d is the number of spatial dimensions in which the organism forages. This dependence arises because the evolutionary setting of the selection gradient on body mass at evolutionary steady state is functionally dependent upon the exponent of the allometric relationship between body mass and the organisms ability to exploit the resource, and because the density-dependent constraints of competitive interactions and local resource exploitation suggest that this exponent is evolutionarily determined by the spatial dimensionality of the foraging behaviour (Witting 1995). The dependence of the allometric expo-

nents in mobile organism on the dimensionality of the foraging behaviour is supported empirically (Witting 1995, 1997), while the observed transitions in the allometric exponents are left unexplained by other resent hypotheses on the evolution of body mass exponents (Kozłowski and Weiner 1997; West et al. 1997; Witting 1998; Brown and West 2000).

Both the evolutionary equilibrium and the evolutionary steady state are based on the assumption that the body mass can evolve to limits where it can absorb the amount of energy required to maintain the interactive competition at the levels of the two equilibria. If instead there is an upper limit to the body mass and this limit is below the body mass at evolutionary equilibrium or evolutionary steady state, we can expect that the extra energy available from the energetic state of the organism will be allocated into enhanced reproduction generating population growth beyond the expectations of the two equilibria. I refer to this equilibrium as the upward constrained equilibrium, a case where we can expect an enhanced level of interactive competition. And at the upper limit, where the upper limit to body mass is very much lower than the body mass suggested by the evolutionary equilibria and the energetic state of the organism, we can expect that the level of interactive competition in the population goes toward infinity, i.e., that $\iota \to \infty$.

Hence the selection pressure of density-dependent competitive interactions can be expected to equilibrate the body mass at four evolutionary states, where the evolutionarily determined level of interactive competition (ι^{*e}) associated with these states are

$$
\iota^{*e} = \begin{cases} 0 & \text{if} \quad \iota^{*e} = \iota^{*i} \\ \frac{1}{\psi_w} & \text{if} \quad \iota^{*e} = \iota^{**} \\ \frac{4d-1}{(2d-1)\psi_w} & \text{if} \quad \iota^{*e} = \iota^{*s} \\ \infty & \text{if} \quad \iota^{*e} = \iota^{*c} \end{cases} \tag{29}
$$

where $*i$ is the evolutionary state of a negligible body mass expected to evolve in organisms at the lowest energetic state ($\epsilon \approx 0$), $**$ is the evolutionary equilibrium of a non-negligible body mass expected to evolve in organisms with a high and stable energetic state ($\epsilon \gg 0 \wedge d\epsilon/dt = 0$), $*s$ is the evolutionary steady state for a non-negligible body mass that increases exponentially, a state expected to evolve in organisms with a high and exponentially increasing energetic state ($\epsilon \gg 0 \wedge d\epsilon/dt = \rho\epsilon$, with ρ being a constant), and $*c$ is the evolutionary state of a non-negligible body mass that is upward constrained relative to the energetic state of the organisms. For the evolutionary state $*c$, the interactive level $\iota^{*c} = \infty$ is an upper limit. More generally, $\iota^{*c} \gg \iota^{*s}$, but the upper limit is used in this paper in order to cover the full range of interactive levels. The four evolutionary states of eqn 29 are denoted $*i$, $**$, $*s$, and $*c$ because it is shown in the next sections that they correspond with the four phenotypic states of Table 2.

3.2 Interacting unit

For low-energy organisms at evolutionary state $*i$ we find from eqn 18 that $\partial r^*/\partial z < 0$ and that $\partial r^*/\partial n < 0$. The evolutionarily stable attractor is thus an interacting unit formed by a single individual ($z^{*i} = 0$ and $n^{*i} = 1$).

For high-energy organisms the selection gradient on the tightness of the interacting unit is

$$
\left.\frac{\partial r_i^*}{\partial z_i}\right|_{z_i=z} = \frac{\psi_z \iota^{*e}}{z} - \frac{n-1}{n-(n-1)z} \tag{30}
$$

by eqn 22. The equilibrium for the fully co-operating interacting unit is the size that is in evolutionary equilibrium for $z = 1$. Thus, setting $z = 1$ in eqn 30 and solving for n the equilibrium number of individuals per interacting unit is $n^{*e} = \psi_z \iota^{*e} + 1$. Inserting ι^{*e} from eqn 29 into this equation, for the symmetrical case $\psi_z = \psi_w$ we find that

$$
n^{*e} = \begin{cases} 1 & \text{if} \quad \iota^{*e} = \iota^{*i} \\ 2 & \text{if} \quad \iota^{*e} = \iota^{**} \\ \approx 3 & \text{if} \quad \iota^{*e} = \iota^{*s} \\ \infty & \text{if} \quad \iota^{*e} = \iota^{*c} \end{cases} \tag{31}
$$

of which the three equilibria for high-energy organisms are evolutionarily stable attractors because

$$
\begin{aligned}
\left.\frac{\partial^2 r_i^*}{\partial z_i^2}\right|_{z_i=z=z^{*e}} &= \left.\frac{\partial}{\partial z}\left(\left.\frac{\partial r_i^*}{\partial z_i}\right|_{z_i=z}\right)\right|_{z=z^{*e}} \\
&= \begin{cases} -2 & \text{if} \quad \iota^{*e} = \iota^{**} \\ -\frac{12d-5}{2d-1} & \text{if} \quad \iota^{*e} = \iota^{*s} \\ -\infty & \text{if} \quad \iota^{*e} = \iota^{*c} \end{cases}
\end{aligned} \tag{32}
$$

Relative to the symmetrical case the interacting unit of high-energy organisms will increase when the tightness of the interacting unit is a more significant interactive trait than body mass (i.e., when $\psi_z > \psi_w$), while the interacting unit will decline when the opposite is the case. For $\psi_z = 2\psi_w$, e.g., we expect a two-fold increase in the interacting unit.

3.3 Reproducing unit

For low-energy organisms at evolutionary state $*i$ we find from eqn 18 that $\partial r^*/\partial \epsilon_\varphi < 0$, that $\partial r^*/\partial \varphi < 0$,

and that $\partial r^*/\partial n < 0$. The evolutionarily stable attractor is thus a reproducing unit with a single replicating individual and no non-replicating individuals ($\epsilon_\varphi^{*i} = 0$, $\varphi^{*i} = 0$, and $n^{*i} = 1$).

For high-energy organisms the joint selection gradient on the existence (ϵ_φ) and proportion (φ) of non-replicating individuals is

$$\left.\frac{\partial r_i^*}{\partial \epsilon_{\varphi_i}\varphi_i}\right|_{\epsilon_{\varphi_i}\varphi_i=\epsilon_\varphi\varphi} = \frac{\psi_{\epsilon_\varphi\varphi}\iota^{*e}}{\epsilon_\varphi\varphi} - \frac{1}{1-\epsilon_\varphi\varphi} \quad (33)$$

by eqn 22. The evolutionary equilibrium in the fraction of fully evolved non-replicating individuals is the equilibrium fraction φ for $\epsilon_\varphi = 1$. Setting $\epsilon_\varphi = 1$ in eqn 33 and solving for φ the fraction of non-replicating individuals per interacting unit is $\varphi^{*e} = \psi_{\epsilon_\varphi\varphi}\iota^{*e}/(1+\psi_{\epsilon_\varphi\varphi}\iota^{*e})$. Inserting ι^{*e} from eqn 29 into this equation, for the symmetrical case $\psi_{\epsilon_\varphi\varphi} = \psi_w$ we find that

$$\varphi^{*e} = \begin{cases} 0 & \text{if} \quad \iota^{*e} = \iota^{*i} \\ 1/2 & \text{if} \quad \iota^{*e} = \iota^{**} \\ \approx 2/3 & \text{if} \quad \iota^{*e} = \iota^{*s} \\ 1 & \text{if} \quad \iota^{*e} = \iota^{*c} \end{cases} \quad (34)$$

of which the three equilibria for high-energy organisms are evolutionarily stable attractors because

$$\left.\frac{\partial^2 r_i^*}{\partial\varphi_i^2}\right|_{\varphi_i=\varphi=\varphi^{*e}} = \left.\frac{\partial}{\partial\varphi}\left(\left.\frac{\partial r_i^*}{\partial\varphi_i}\right|_{\varphi_i=\varphi}\right)\right|_{\varphi=\varphi^{*e}} \quad (35)$$
$$= \begin{cases} -8 & \text{if} \quad \iota^{*e} = \iota^{**} \\ -\frac{108d-45}{8d-4} & \text{if} \quad \iota^{*e} = \iota^{*s} \\ -\infty & \text{if} \quad \iota^{*e} = \iota^{*c} \end{cases}$$

For each of the four evolutionary states of eqns 31 and 34 there is one, and only one, replicating individual per interacting unit, while the remaining 0, 1, 2, and ∞ individuals for the different evolutionary states are non-replicating. This implies that each of the four possible interacting units of eqn 31 contain a single, and only a single, reproducing unit.

Relative to the symmetrical case the fraction of non-replicating individuals in high-energy organisms will increase when the non-replicating individuals are interactively more significant than body mass (i.e., when $\psi_{\epsilon_\varphi\varphi} > \psi_w$), while the fraction will decline when the opposite is the case. It may also be worth noting that if $\psi_{\epsilon_\varphi\varphi} = \psi_z \neq \psi_w$, then, from the last two sections, it can be seen that all the interacting units of high-energy organisms will contain only a single reproducing unit, while it is the number of non-replicating individuals that will differ from the numbers indicated by eqns 31 and 34.

3.4 Sexual unit

Asexually produced offspring workers

For the case of asexually produced offspring workers the interactive quality of sexual reproduction can be given by the number of sexual males n_ϕ, while the cost of sexual reproduction is $\ln(1-\phi)$ by eqn 13. Thus, as $\phi = n_\phi/(n_\phi + n_\theta)$, from eqn 22, the fitness profile of sexual reproduction can be given as

$$r_i^* = \ln[n_\theta/(n_{\phi,i}+n_\theta)]+\psi_{n_\phi}\iota^*(\ln n_{\phi,i}-\ln n_\phi)+\rho \quad (36)$$

where $\rho = \ln(p\epsilon^*[1-\epsilon_\varphi\varphi][1-(n-1)z/n]/w)$. For low-energy organisms at evolutionary state $*i$, with $\iota^{*i} = 0$, we find from eqn 36 that $\partial r^*/\partial n_\phi < 0$. The evolutionarily stable attractor is thus asexual reproduction with no sexual males ($n_\phi^{*i} = 0$) and the fathers fraction of the offspring's genome being zero ($\phi^{*i} = 0$).

For high-energy organisms the selection gradient on the number of sexual males is

$$\left.\frac{\partial r_i^*}{\partial n_{\phi_i}}\right|_{n_{\phi_i}=n_\phi} = \frac{\psi_{n_\phi}\iota^{*e}}{n_\phi} - \frac{1}{n_\phi + n_\theta} \quad (37)$$

In this case we have from eqn 29 that $\psi_w\iota^{*e} \geq 1$ and thus $\partial r_i^*/\partial n_{\phi_i}|_{n_{\phi_i}=n_\phi} > 0$ when $\psi_{n_\phi} \approx \psi_w$. This implies that there is selection against asexually produced offspring workers, and that the equilibrium fraction of sexual males is identical with the equilibrium fraction of non-replicating individuals [eqn 34]. It is thus only high-energy organisms at the evolutionary equilibrium that have the usual form of sexual reproduction, where there is a single father and where half of the offspring's genome comes from the father while the other half comes from the mother. For organisms at evolutionary steady state we predict two fathers with the fathers' fraction being 2/3, and at the constrained equilibrium the number of fathers goes to infinity while the fathers' fraction of the offspring's genome approaches one.

Sexually produced offspring workers

The cost of sexual reproduction is the same $[\ln(1-\phi)]$ no matter whether the offspring workers are produced asexually or sexually. Asexual reproduction is thus the evolutionary stable attractor of low-energy organisms independently of whether the potential production of offspring workers is sexual or asexual.

As the cost of sex is independent of the production of offspring workers, and as the interactive quality that can be gained through sexual reproduction is largest for sexually produced offspring workers [eqns 14 and 17], for high-energy organisms with interactive competition we can expect selection for sexually produced

offspring workers at the cost of asexually produced offspring workers. But can the interactive quality of sexually produced offspring workers relative to that of asexually produced offspring workers be so high that sexually produced offspring workers can evolve at the cost of some of the sexual males?

With sexually produced offspring workers the interactive quality of sexual reproduction can be given as $n\phi$ and the fitness profile as

$$r_i^* = \ln(1 - \phi_i) + \psi_{n\phi}\iota^*[\ln(n_i\phi_i) - \ln(n\phi)] + \rho \quad (38)$$

with ρ defined in eqn 36. Note here that the cost of sex to a given female variant is given exclusively by the ϕ parameter, while the interactive quality that she can gain through sex is given by $n\phi$. The latter two parameters act as a single trait because the quality that can be gained through the sexual parameter ϕ depends on the number of sexually produced offspring workers and thus on the size of the interacting unit. Hence, to obtain the selection gradient we need to differentiate the fitness cost $[\ln(1 - \phi_i)]$ with respect to ϕ_i, while the fitness gained through interactive competition $(\psi_{n\phi}\iota^*[\ln(n_i\phi_i) - \ln(n\phi)])$ needs to be differentiated with respect to $n_i\phi_i$. Thus, the selection gradient is

$$\left.\frac{\partial r_i^*}{\partial \phi_i}\right|_{\phi_i=\phi}^{\text{Cost}} + \left.\frac{\partial r_i^*}{\partial n_i\phi_i}\right|_{n_i\phi_i=n\phi}^{\text{Gain}} = \frac{\psi_{n\phi}\iota^{*e}}{n\phi} - \frac{1}{1-\phi} \quad (39)$$

and the evolutionary equilibrium $\phi^{*e} = \psi_{n\phi}\iota^{*e}/(n + \psi_{n\phi}\iota^{*e})$. For the symmetrical case $\psi_w = \psi_{n\phi}$, the three equilibria of high-energy organisms are evolutionarily stable attractors because

$$\left.\frac{\partial^2 r_i^*}{\partial \phi_i^2}\right|_{\phi_i=\phi=\phi^{*e}}^{\text{Cost}} + \left.\frac{\partial^2 r_i^*}{\partial (n_i\phi_i)^2}\right|_{n_i\phi_i=n\phi=n^{*e}\phi^{*e}}^{\text{Gain}} \quad (40)$$

$$= \left.\frac{\partial}{\partial \phi}\left(\left.\frac{\partial r_i^*}{\partial \phi_i}\right|_{\phi_i=\phi}\right)\right|_{\phi=\phi^{*e}}^{\text{Cost}}$$

$$+ \left.\frac{\partial}{\partial n\phi}\left(\left.\frac{\partial r_i^*}{\partial n_i\phi_i}\right|_{n_i\phi_i=n\phi}\right)\right|_{n\phi=n^{*e}\phi^{*e}}^{\text{Gain}}$$

$$= \begin{cases} -9/2 & \text{if} \quad \iota^{*e} = \iota^{**} \\ -\frac{(10d-3)^2}{(4d-1)(6d-2)} & \text{if} \quad \iota^{*e} = \iota^{*s} \\ -\infty & \text{if} \quad \iota^{*e} = \iota^{*c} \end{cases}$$

From eqn 30 the number of individuals in the interacting unit is $n^{*e} = \psi_z\iota^{*e} + 1$. This implies that the equilibrium fraction of sexual males, and the equilibrium fraction of the father/s genome in the offspring, is

$$\phi^{*e} = \frac{\psi_{n\phi}\iota^{*e}}{\iota^{*e}(\psi_{n\phi} + \psi_z) + 1} \quad (41)$$

And as the number of sexual males per interacting unit is $n_\phi^{*e} = \phi/(1 - \phi)$ for the predicted case with a single replicating female, we find that the number of sexual males per interacting unit is

$$n_\phi^{*e} = \frac{\psi_{n\phi}\iota^{*e}}{\psi_z\iota^{*e} + 1} \quad (42)$$

Thus, when $\psi_{n\phi}\iota^{*e} \leq \psi_z\iota^{*e} + 1$ we never expect more than a single male per female. And for the four evolutionary states $*i$, $**$, $*s$, and $*c$ of the symmetrical case $\psi_z = \psi_{n\phi} = \psi_w$, we expect respectively 0, 0.5, ≈ 0.7, and 1 sexual males per sexual female.

For the more natural case where the composition of individuals in the interacting unit is determined by quanta of whole individuals we obtain a slightly different result. Here, sexually produced offspring workers cannot be produced before the interacting unit contains both a female and a male. Thus, for the case of non-negligible body masses in evolutionary equilibrium ($**$), where the number of individuals in the interacting unit is two, the non-replicating individual will either be an asexually produced offspring worker or a sexually reproducing male. Thus, from eqn 37, we expect sexual reproduction between a female and a single male. And for the evolutionary steady state ($*s$) we need to round 0.7 to 1, so that the expected number of sexual males per interacting unit is

$$n_\phi^{*e} = \begin{cases} 0 & \text{if} \quad \iota^{*e} = \iota^{*i} \\ 1 & \text{if} \quad \iota^{*e} = \iota^{**} \\ 1 & \text{if} \quad \iota^{*e} = \iota^{*s} \\ 1 & \text{if} \quad \iota^{*e} = \iota^{*c} \end{cases} \quad (43)$$

while the number sexually produced offspring workers is

$$n_w^{*e} = \begin{cases} 0 & \text{if} \quad \iota^{*e} = \iota^{*i} \\ 0 & \text{if} \quad \iota^{*e} = \iota^{**} \\ 1 & \text{if} \quad \iota^{*e} = \iota^{*s} \\ \infty & \text{if} \quad \iota^{*e} = \iota^{*c} \end{cases} \quad (44)$$

It is thus suggested that density-dependent competitive interactions select for the usual form of sexual reproduction that occurs between one male and one female, and that this occurs at the cost of sexual reproduction at higher levels with more than a single male per female. It is also suggested that sexually produced offspring workers and kin selection may evolve by density-dependent competitive interactions when the equilibrium number of individuals in the interacting unit increases above two, as it is the case at the evolutionary steady state and the constrained evolutionary equilibrium. As the results of eqns 43 and 44 are based on rounded numbers

they hold also for small deviations away from the symmetrical case where the competitive games are similar for all interacting traits.

4 Discussion

4.1 Interacting unit

Interacting units formed by individuals are groups of individuals that co-operate in their interactions with their environment. But individuals on a uniform resource may not be expected to form groups because local resource exploitation within the group is costly to the individuals that form the group.

It was shown that selection by density-dependent competitive interactions among interacting units can outbalance the cost of group formation imposed by local resource exploitation when individuals co-operate to increase the interactive quality of the interacting unit. In this scenario it is the level of interactive competition among the interacting units that determines the optimal group size, and four potential levels of interactive competition are predicted by selection by density-dependent competitive interactions. Low-energy organisms with negligible body masses have negligible interactive competition and the optimal group size is a single individual. High-energy organisms with non-negligible body masses at the evolutionary equilibrium, the evolutionary steady state, and the upward constrained equilibrium, on the other hand, have interactive competition at levels that coincide with optimal group sizes of respectively two, three, and up to infinitely many individuals. These numbers relate to the symmetrical case where the competitive games for group size and body mass are the same.

4.2 Reproducing unit

Interacting units with n individuals can contain from 1 to n reproducing units. A reduction in the number n_θ of reproducing units below n is possible through the evolution of non-replicating individuals like males and non-reproducing offspring. But $n_\varphi = n - n_\theta$ non-replicating individuals per interacting unit is $(n_\varphi + 1)/n_\theta$-fold costly due to the cost of non-replication and, thus, the number of reproducing units may not be expected to evolve below n.

It was shown that selection by density-dependent competitive interactions among interacting units can outbalance the cost of non-replication in $n-1$ of the n individuals in the interacting unit, given that interacting and reproducing units evolve as traits that increase the interactive quality of the interacting unit. With similar competitive games among traits, the predicted interacting units contain a single reproducing unit with the number of non-replicating individuals in the reproducing unit being a function of the level of interactive competition. Thus, the predicted transitions in the level of selection coincide with transitions in the number of individuals per reproducing unit.

The predicted transitions between reproducing units that contain a single, two, three, and up to an infinite number of individuals is given by a selection process where the number of non-replicating and replicating individuals per interacting unit is a function of the level of interactive competition in the population. This hypothesis suggests that large reproducing units, like those of eusocial colonies, evolve in species where the body mass has been evolutionarily constrained relative to the exploitation efficiency. Thus, as an ecto-skeleton may impose an upper constraint on body mass it may not be surprising that full-blown eusociality with thousands of workers per colony is known only from insects.

The constraint on the body mass that can promote the evolution of large reproducing units need not be a physiological or genetical constraint. The constraint may also be environmentally imposed if the species live in narrow canals where selection operates against large-bodied individuals. This type of environmentally imposed constraint might be one reason why eusociality has evolved in the naked mole rat that lives in subterranean canals (Jarvis 1981), and in snapping shrimps that live in sponge canals in coral-reefs (Duffy 1996).

An absolute constraint on body mass is also not necessary. The essential requirement for the evolution of a large reproductive unit is only that the body mass be constrained relative to the assimilation of resource. In this case the organism will have a surplus of energy to allocate into reproduction generating an increase in the number of intra-specific competitive interactions. Indeed a relative constraint on body mass might be a promising hypothesis for eusociality, because it seems that eusociality has evolved mainly in those insect taxa that explore plentiful resources that are relatively easy to collect.

Selection by density-dependent competitive interactions suggests that males, helpers in co-operative breeders, and workers in eusocial species evolve as individuals that specialise in interactive competition at the cost of replication. More traditional studies on the evolution of males have considered an evolutionary transition from individuals that produce macrogametes to individuals that produce microgametes. Microgametes may evolve to ensure that cytoplasmic inheritance oc-

curs only through the female line (Cosmides and Tooby 1981; Law and Hutson 1992; Bulmer 1994). This may prevent the spread of harmful cytoplasmic parasites and/or the evolution of selfish cytoplasmic organelles. Another explanation assumes that it is difficult for gametes to find partners, and that large zygotes have a great advantage over smaller zygotes (Parker et al. 1972; Maynard Smith 1978; Hoekstra 1980, 1984, 1987; Hoekstra et al. 1984; Cox and Sethian 1985; Dusenbery 2000). The microgametes, or sperm, are then designed to solve the gamete encounter problem, and the macrogametes, or eggs, to guarantee the success of the zygote. These models generally assume that the fully evolved male contributes to reproduction only by the transmission of microgametes to the female. This implies that the male is evolutionarily unstable due to his two-fold cost, and that we may expect hermaphrodites instead of dioecious organisms. But the model with density-dependent competitive interactions predicts an evolutionarily stable male because the fitness gained through the interactive action of the male outbalances not only the two-fold cost of the male, but also the two-fold cost of meiosis.

4.3 Sexual unit

The replicating individual in a reproducing unit of n individuals can have asexual reproduction or sexual reproduction with 1 to $n-1$ of the $n-1$ non-replicating individuals. Sexual reproduction between the replicating and $1 \leq n_\phi \leq n-1$ non-replicating individuals is possible when the replicating individual evolves into a female, the n_ϕ non-replicating individuals evolve into males, and all sexual individuals transfer $1/(n_\phi + 1)$ fractions of their heritable code to each sexually produced offspring. But sexual reproduction between a female and n_ϕ males is $(n_\phi + 1)$-fold costly because of the diluted transfer of genes and, thus, sexual reproduction may not be expected to evolve.

It was shown that selection by density-dependent competitive interactions among interacting units may outbalance the cost of sexual reproduction given that interacting, reproducing, and sexual units evolve as traits that enhance the interactive quality of the interacting unit. But sexual reproduction can evolve by the suggested mechanism only if the level of interactive competition is sufficiently high. For the proposed model it is the predicted increase in interactive competition associated with the transition from low-energy organisms with negligible body masses to high-energy organisms with large body masses that can explain the evolutionary transition from asexual reproduction to the usual form of sexual reproduction with a single male per female and a two-fold cost of meiosis.

If offspring workers can be produced only asexually, selection by density-dependent competitive interactions predicts unknown forms of sexual reproduction where $n-1$ males mate with a single female and the sexually produced offspring receive genes from n parents. But more generally, offspring workers may evolve to be produced also by sexual reproduction. And with density-dependent competitive interactions we expect sexually produced offspring workers because they can inherit interactive quality from the sexual male, while at the same time the cost of sex is unaffected by a transition from asexually to sexually produced offspring workers. The cost of sex pertain only to the reproductive lineage, where the probability that a particular gene is copied into the future declines with a transition from asexually produced reproducing offspring to sexually produced reproducing offspring.

With sexually produced offspring workers the proposed model suggests that the sexual unit in pair-wise, co-operative, and eusocially reproducing organisms is a single male per female with a two-fold cost of meiosis, instead of any other number of males per female and any other level of cost. Sexual units with more than two individuals are not expected to evolve for the case of sexually produced offspring workers because the interactive quality of the male is transferred to the sexually produced offspring workers. This generates a diminishing return where the interactive quality that can be gained by exchanging an offspring worker with a sexual male is a declining function of the number of males per female. It is only for the initial transition from asexual to pair-wise sexual reproduction that the interactive quality of the male can outbalance the cost of sexual reproduction. For all potential remaining transitions, the transfer of male interactive quality to sexually produced offspring workers implies that the interactive quality that can be gained by exchanging an offspring worker with an additional sexual male cannot outbalance the extra cost to sexual reproduction associated with that transition.

The suggested evolution of pair-wise sexual reproduction implies that sexually produced offspring workers and kin selection evolve as a balance between the cost of sexual reproduction and the overall interactive quality of the interacting unit. In result, the expected number of sexually produced offspring workers per reproducing unit becomes a function of the level of interactive competition. The optimum is zero workers for low-energy organisms and high-energy organisms with body masses in evolutionary equilibrium, while it is one and up to

an infinite number of workers for high-energy organisms with body masses at respectively the evolutionary steady state and the upward constrained equilibrium. Under the proposed model, sexually produced offspring workers and kin selection are the evolutionary results of large interacting units instead of being the traits that induce the evolution of large interacting units.

This paper has dealt with mobile organisms, but density-dependent competitive interactions may also play a role in explaining why sexual reproduction tends to occur among hermaphrodites when the organism is sessile. In contrast to dioecious organisms hermaphrodites can avoid the four-fold cost of sex. It is thus likely that the widespread transition from dioecious to hermaphroditic sexual reproduction between mobile and sessile organisms is caused by a selection transition where selection can outbalance the costs of sex in mobile organisms but not in sessile organisms. Such a selection transition exists for selection by density-dependent competitive interactions. It was showed that selection by density-dependent competitive interactions can outbalance the costs of sex in mobile organisms when the co-operative act of sexual reproduction between a female and a male increases the interactive quality of the interacting unit. In this framework there is selection for an interacting unit at the level of the reproducing unit and at a level higher than or equal to the level of the sexual unit. If instead the interacting unit is constrained at the individual level it implies that females and males cannot co-operate to increase the fitness of units with more than one individual and, thus, in such instances sexual reproduction cannot evolve as a trait of co-operation between females and males. It is thus intriguing that the interacting unit of competitive interactions in sessile organisms generally is constrained at the individual level because sessile organisms compete for resources that are provided by a flowing medium. This means that sessile organisms compete by position in the resource flow with the position and size of the individual organism being the essential traits that define the interactive quality of the interacting unit. In consequence a sessile male cannot compete for a sessile female unless he will also compete against her. The evolutionary optimum of competitive interactions to sexual reproduction in sessile organisms is thus hermaphroditic individuals that avoid the costs of sex experienced by sessile dioecious organisms.

In relation to general differences in the mode of sexual reproduction between sessile and mobile organisms we may also note that there is no male choice in hermaphroditic sessile organisms to prevent that asexual reproduction and self-fertilisation evolve in order to enhance the intrinsic growth rate of the hermaphrodite. This may explain why asexual reproduction and self-fertilisation are widespread in sessile sexual organisms, while these traits are rare to absent in mobile sexual organisms.

In conclusion the proposed model suggests that male individuals, sexual reproduction, and a diploid genome evolved in high-energy mobile organisms where selection by density-dependent competitive interactions outbalances both the two-fold cost of the male and the two-fold cost of meiosis. Thereafter some of these organisms became sessile and then they evolved into hermaphrodites in order to avoid the costs of sex.

Sexual selection

The selection pressure of density-dependent competitive interactions suggests that there is sexual selection on the mode of sexual reproduction. This form of sexual selection occurs by means of a female choice for interactively superior males and a male choice for females that allocate the largest fraction of the male genome to the offspring. This causal relationship, where sexual selection arises from secondary sex traits and selects on the mode of sexual reproduction, is opposite to the causal relation originally proposed by Darwin (1859, 1871). According to the original proposal and apparently all subsequent studies (Andersson 1994), sexual selection is an intermediate form of selection that arises from sexual reproduction and selects on secondary sex traits by means of mate choice or intrasexual contest for the opposite sex.

The models that support Darwin's sexual selection hypothesis are usually divided into the Fisherian run away process (Fisher 1930) and indicator mechanisms (e.g., Fisher 1915; Williams 1966b; Maynard Smith 1976; Zahavi 1975; Hamilton 1982; Hamilton and Zuk 1982; Heywood 1989; Hoelzer 1989; Grafen 1990, reviewed Andersson 1994), also known as the good gene or handicap hypothesis. Several authors have shown that these two sexual selection mechanisms may lead to the evolution of energetically costly secondary sex traits. But most of the predictions are evolutionarily unstable in the way that the mechanisms fail to explain the evolution of energetically costly secondary sex traits at the expense of energetically non-costly secondary sex traits. If we allow for genetic variation in the energetic cost of the secondary sex trait, and costly and non-costly traits are potentially equally suited as indicators for female choice, then most of these models predict the evolution of non-costly secondary sex traits. This contrast to many species that have an energetic

cost associated with secondary sexual characters (Andersson 1994). Energetically costly secondary sex traits that evolve by density-dependent competitive interactions for other resources than mates, however, tend to be evolutionarily stable. The requirement is that the individuals that invest less energy in the secondary sex traits tend to lose during competitive interactions with individuals investing more energy. This condition is fulfilled when the secondary sex traits are direct measures of interactive ability.

4.4 Conclusion

It was shown that density-dependent competitive interactions among interacting units represent a general and relatively simple mechanism that can explain evolutionary transitions from asexual over pair-wise sexual to eusocial reproduction. In the phenotypic space of potential reproductive modes where individuals may replicate asexually on their own or by sexual reproduction involving a single to an infinite number of individuals with the remaining individuals of the interacting unit being either asexually or sexually produced offspring workers, the proposed model equilibrates at four reproductive modes that are widespread among natural organisms.

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A   Age-structure

Making a few simplifying assumptions, in this appendix the life history model of eqn 13, i.e.,

$$\lambda^* = p\epsilon^*\beta \tag{45}$$

with

$$\beta = [1 - \phi][1 - \epsilon_\varphi \varphi][1 - (n-1)z/n]/w \tag{46}$$

is deduced from a larger class of age-structured models. Let subscript a denote age class a, let age-structured survival p_a be density independent, and let age-structured reproduction m_a be determined by the age structure in the amount of energy available for reproduction $\tilde{\epsilon}_a$ and the life history component β that is assumed to be independent of age. Then, $m_a = \tilde{\epsilon}_a \beta$, and if ϵ_a is the energy available at zero population density and $f(N)$ is the density regulation function, we find that

$$m_a = \epsilon_a \beta f(N) \tag{47}$$

Let the density regulation function $f(N)$ operate independent of age so that lifetime reproduction is

$$R = \epsilon \beta f(N) \tag{48}$$

with $\epsilon = \sum_{a=0}^{T} \epsilon_a$ being the energy available for reproduction at zero population density during the complete life span for individuals that die of senescence in age-class T. Net lifetime reproduction is then

$$R_0 = \beta f(N) \sum_{a=0}^{T} l_a \epsilon_a \tag{49}$$

with $l_a = \prod_{a=0}^{a-1} p_a$ and $l_0 = 1$. Now, let the survival scalar p in eqn 45 be defined as $p = R_0/R$. Then, from eqns 48 and 49

$$p = \epsilon^{-1} \sum_{a=0}^{T} l_a \epsilon_a \tag{50}$$

Hence, from eqn 50, $\sum_{a=0}^{T} l_a \epsilon_a = p\epsilon$ and, thus, from eqn 49 net lifetime reproduction is

$$R_0 = p\epsilon \beta f(N) \tag{51}$$

At population dynamic equilibrium we have that $\epsilon^* = \epsilon f(N^*)$ and that $R_0^* = \lambda^* = 1$ and, thus, from eqn 51 that

$$\lambda^* = p\epsilon^*\beta \tag{52}$$