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Stable eusociality via maternal manipulation when resistance is costless

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Monday 25th May, 2015

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Keywords: Parent-offspring conflict, altruism, maternal effects, pheromone.

Running title: Stable eusociality via maternal manipulation.

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Abstract

In many eusocial species, workers develop or maintain their non-reproductive condition following maternal influence through aggression, differential feeding, or pheromones. This observation has suggested that eusociality may evolve from maternal manipulation where the mother induces offspring to take worker roles against their inclusive fitness interests. If manipulation is executed via aggression or poor feeding, offspring resistance to manipulation could be costly enough to be disfavored, allowing eusociality via manipulation to be evolutionarily stable. However, if manipulation is executed via pheromones, resistance could be less costly, in principle leading to evolutionarily unstable eusociality. Here I show that maternal manipulation can generate evolutionarily stable eusociality even if resistance has no direct costs provided that maternally neglected offspring use help more efficiently than maternally provisioned offspring (e.g., to regain survival). Manipulation temporarily creates ineffectively resisting helpers that allow the mother to reduce maternal care toward helped offspring. If maternally neglected offspring use help more efficiently, maternal care reduction produces offspring that benefit more from the ineffectively resisting helpers. Thus, maternal care reduction increases the average benefit received by helped offspring, bringing Hamilton's rule to satisfaction and eliminating selection for resistance. Manipulation can then generate stable eusociality under smaller benefit-cost ratios than when manipulation is absent although resistance is costless. These results predict that eusociality where ignoring maternal influence is rather costless is likely to have originated from maternal manipulation if (1) maternally neglected offspring are highly efficient help users and (2) maternally provisioned offspring can only moderately increase their survival by being helped.

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Introduction

Eusocial organisms form colonies that are distinctly influenced by their queens. In many species, a eusocial colony is composed of one queen with largely non-reproductive workers that are the queen's offspring (Wilson, 1971, Michener, 1974). Whether a queen's offspring becomes a worker or a future queen is often mediated by the queen herself: for example, (1) in some social wasps and bees the queen maintains the reproductive monopoly of the colony through aggression (Fletcher and Ross, 1985), (2) in many social insects the queen can feed offspring with food of different quantity or quality influencing offspring's future reproductive caste (i.e., queen or worker) (e.g., O'Donnell, 1998, Bourke and Ratnieks, 1999, Kapheim *et al.*, 2011, Brand and Chapuisat, 2012); (3) in an ant species the queen can deposit hormones in the eggs that induce such offspring to develop into workers (Schwander *et al.*, 2008); (4) in certain wasp and termite species the queen can produce pheromones that prevent offspring from becoming queens (Bhadra *et al.*, 2010, Matsuura *et al.*, 2010); and (5) in honeybees queen pheromones alter workers' brain functioning (Beggs *et al.*, 2007) and induce workers to feed larvae without royal jelly which causes larvae to develop into workers (Le Conte and Hefetz, 2008, Kamakura, 2011). In addition to influencing caste determination, in many social insects queens can use pheromones to keep workers' ovaries undeveloped so that workers remain non-reproductive (e.g., Holman *et al.*, 2010, Van Oystaeyen *et al.*, 2014). Although environmental temperature, colony size, colony age, as well as other environmental factors and genetic predispositions in the queen's offspring can influence offspring's reproductive status (Lo *et al.*, 2009, Schwander *et al.*, 2010), substantial queen influence in workers is widespread in eusociality.

The function of queen influence is typically interpreted in terms of either manipulation or honest signaling (Dawkins and Krebs, 1978, Keller and Nonacs, 1993). Manipulation

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refers to altering a recipient individual's phenotype against the inclusive fitness interests of the recipient (Dawkins, 1978, 1982), a possibility increasingly well documented for parasites that manipulate their hosts (Poulin, 2010, Maure *et al.*, 2011, 2013, Dheilly *et al.*, 2015). In contrast, signaling refers to altering a recipient's phenotype provided that the signal "evolved because of that effect, and which is effective because the receiver's response also evolved" (Maynard Smith and Harper, 2003). Honest signaling thus requires that altering a recipient's phenotype is in the inclusive fitness interests of the recipient (Maynard Smith and Harper, 2003). So, on the one hand, if in a given case the observed queen influence is manipulation, the population is expected to be in one of three possible stages: in an ongoing arms race between manipulation and resistance to manipulation, in an equilibrium with some acquiescence to manipulation if resistance is costly enough, or in an equilibrium with zero acquiescence to manipulation if resistance is sufficiently costless (e.g., Trivers, 1974, Craig, 1979, Uller and Pen, 2011, González-Forero and Gavrilets, 2013). On the other hand, if queen influence is honest signaling, for example of queen fertility, the queen influence and offspring response are expected to evolve in a mutually beneficial way (Keller and Nonacs, 1993, Maynard Smith and Harper, 2003). Then, a key factor allowing to distinguish whether queen influence is manipulation or honest signaling is how costly resistance would be: if resistance is rather costless and no arms race is detected, then the queen influence is more likely to be honest signaling (Keller and Nonacs, 1993). When queen influence is executed via pheromones, ignoring queen pheromones is thought to incur somewhat small direct fitness costs (Keller and Nonacs, 1993). Hence, queen influence via pheromones has been suggested to more likely constitute honest signaling than manipulation (Keller and Nonacs, 1993). Indeed, evidence is increasingly viewed as supporting the notion that queen pheromones honestly signal the queen's

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reproductive health (e.g., Heinze and d'Ettorre, 2009, van Zweden *et al.*, 2014).

The widespread occurrence of queen influence in eusocial taxa has suggested that queen influence may have a role in how eusociality tends to originate (Alexander, 1974, Michener and Brothers, 1974, Linksvayer and Wade, 2005, Russell and Lummaa, 2009). If in a given origin of eusociality maternal influence has a causal role, maternal influence would thus be manipulation or honest signaling at this origin of eusociality. In the case that maternal influence at an origin of eusociality is honest signaling, the genes for helping would be in the offspring and then offspring control their helping behavior. Helping is then favored when $br > c$ where c is the fitness cost to the helper, b is the fitness benefit to the recipient, and r is their relatedness (Hamilton, 1964, Frank, 1998). In contrast, if maternal influence at an origin of eusociality is maternal manipulation, helping is favored under smaller benefit-cost ratios (e.g., $b/c > 1$ rather than $b/c > 1/r$), ultimately because the costs of helping are paid by the helper rather than by the mother who controls the behavior (Trivers, 1974, Charlesworth, 1978, González-Forero and Gavrilets, 2013). Then, in principle, eusociality could be particularly likely to arise via maternal manipulation. However, a primary mechanism of queen influence is via queen pheromones (e.g., Le Conte and Hefetz, 2008) and evidence suggests that queen pheromones are highly conserved, and may thus be ancestral to eusociality (Van Oystaeyen *et al.*, 2014). If proto-queen pheromones have a manipulative causal role at an origin of eusociality, then given the expectation that ignoring them would be rather costless, such eusociality would be evolutionarily unstable because of the evolution of offspring resistance (Trivers, 1974, Craig, 1979, Keller and Nonacs, 1993, Uller and Pen, 2011). This view that costless resistance should destabilize eusociality via manipulation is suggested by a variety of relevant mathematical models of evolutionary conflict (Ratnieks, 1988, Ratnieks and Reeve,

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1992, Reeve and Keller, 2001, Wenseleers *et al.*, 2003, 2004b,a, Cant, 2006, Ratnieks *et al.*, 2006, Shen and Reeve, 2010, Uller and Pen, 2011, Dobata, 2012, González-Forero and Gavrilets, 2013, González-Forero, 2014).

Nonetheless, mathematical models have found that the evolution of fitness payoffs can reduce, eliminate, or increase evolutionary conflicts of interest (Worden and Levin, 2007, Akçay and Roughgarden, 2011, González-Forero, 2014, Stewart and Plotkin, 2014). In one study, the benefit received by helped individuals was assumed to have a genetic basis because helpers control their helping efficiency. The evolution of the benefit was then found to eliminate the mother-offspring conflict over offspring helping behavior introduced by maternal manipulation, thereby stabilizing eusociality via manipulation (González-Forero, 2014). However, such disappearance of conflict requires that a form of resistance is costly (i.e., helping inefficiency). Because resistance costs are not immediately obvious when the maternal influence occurs via pheromones, it is of particular interest to determine whether there is a feasible way in which the mother-offspring conflict over offspring helping behavior can disappear in the absence of any costs of resistance.

Here I consider an alternative way in which the benefit can evolve and eliminate the mother-offspring conflict over offspring helping behavior. To do so, I consider the ability of a mother to influence her offspring in two ways: (1) by influencing offspring's helping behavior and (2) by influencing offspring's condition when receiving help via reducing maternal care toward them. I thus consider the possibility that maternally neglected offspring use help more efficiently than maternally provisioned offspring: that is, that an offspring that was not previously provisioned by the mother uses a unit of help (e.g., food) more efficiently to regain survival than one that was already provisioned by the mother. I build a mathematical model and find that if maternally neglected offspring use help more

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efficiently than maternally provisioned offspring, then maternal manipulation can generate evolutionarily stable eusociality when there are no direct costs associated with resistance. The reason is that the temporary helpers created by manipulation allow the mother to reduce maternal care toward the offspring that receive help, and since maternally neglected offspring use help more efficiently the average benefit to recipients increases eliminating selection for resistance. Thus, maternal manipulation can generate stable eusociality under smaller benefit-cost ratios than when manipulation does not occur even though there are no direct costs associated with resistance. Results from the model yield testable predictions to discern whether a given instance of eusociality where maternal influence is rather costless to ignore is likely to have originated from maternal manipulation rather than from offspring control of the helping behavior.

Model

Key assumptions

I consider a population with parental care. For concreteness, I take parental care to be brood provisioning, although it can be taken as any form of parental care that is directed toward individual offspring rather than to an entire brood (e.g., brood defense that is directed to individual offspring; Cocroft, 2002). Each mother produces and provisions two subsequent broods, and then dies. The first brood reaches adulthood while the second one is not yet mature, so generations are overlapping. This form of reproduction is common in primitively eusocial paper wasps and sweat bees as well as in their solitary sister taxa (Michener, 1990, Hunt, 2007). Upon reaching adulthood, all adults disperse from their natal nest to a common mating pool. All individuals in the mating pool mate once and

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randomly. This assumption of single mating follows the evidence that monogamy is ancestral to eusociality (Hughes *et al.*, 2008, Boomsma, 2009). After mating, females compete globally for patches with resources to establish their nests. Each successful female secures a patch with resources and allocates the secured resources into producing and provisioning offspring of the two broods, closing the life cycle.

I consider a trait that allows the mother to cause offspring to stay in their natal nest as adults and call it maternal influence (which is a maternal effect trait; Wolf and Wade, 2009). An additional trait allows offspring to resist maternal influence by leaving the natal nest without delay. Thus, the control of offspring behavior is shared between mother and offspring. Finally, an array of three traits describe maternal resource allocation regarding offspring production and maternal care. I thus develop a mathematical model for the coevolution of maternal influence, offspring resistance, and maternal resource allocation.

Maternal influence and offspring resistance occur as follows. The mother has genes that allow her to influence first-brood offspring to stay in the natal nest as adults (e.g., by means of a pheromone). Influenced offspring can acquiesce (i.e., not resist) by staying as adults in their natal nest and by expressing some of their usual parental care behaviors. The parental care behaviors expressed by acquiescing first-brood offspring are received by the available brood which are second-brood offspring (i.e., helping is directed toward full siblings). A somewhat similar form of acquiescence is known in hosts that are manipulated by parasites to perform defense behaviors (Maure *et al.*, 2011, 2013). I will refer to an acquiescing individual as a helper. If a second-brood offspring receives help, its survival increases, where offspring survival is defined as the probability to become a parent. Alternatively, offspring also have genes that allow them to resist the maternal influence by leaving the nest without delay to mate without incurring any direct fitness loss (e.g., by

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reducing the number of binding site receptors of the pheromone; as discussed by Kuijper and Hoyle, 2015). Similar dispersal behaviors are known for first-brood individuals leaving their natal nest in primitively eusocial paper wasps (Reeve *et al.*, 1998) and sweat bees (Yanega, 1988). The effectiveness of resistance to maternal influence is weak at the start of the coevolutionary process because individuals have not been previously exposed to the maternal influence under consideration. Such weak resistance of naive hosts when exposed to novel parasites has been documented experimentally in microorganisms (Lohse *et al.*, 2006).

Maternal resource allocation occurs as follows. The mother controls how much resource to devote to each of the two broods, and out of this resource she controls how much is spent in producing and provisioning offspring. An offspring is either provisioned or not by the mother. I refer to an offspring that is provisioned by the mother as being maternally provisioned and to one not provisioned by the mother as being maternally neglected. These two properties describe an offspring condition. After the mother has had the opportunity to provision offspring, they can be provisioned by helpers; that is, they can be helped. Maternally neglected offspring die if not helped. However, maternally neglected offspring can regain some of their survival by being helped. Such recovery by being helped has been documented in cooperatively breeding birds (Russell *et al.*, 2007). At the start of the coevolutionary process, the mother is favored to provision all of her offspring. This assumption relies on parental care as an accepted precondition for eusociality (Andersson, 1984). The interactions in the model are summarized in Fig. 1. Note that maternal influence does not occur through poor provisioning, as maternally neglected offspring die if not helped (Fig. 1). Indeed, it will be seen that maternal influence is directed toward first-brood offspring while the mother reduces maternal care toward second-brood

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offspring.

The central assumption of the model is the following. I assume that maternally neglected offspring use help more efficiently than maternally provisioned offspring. Consequently, for a given unit of food received from helpers, the survival of maternally neglected offspring increases more than that of maternally provisioned offspring. This assumption relies on the expectation that maternally neglected offspring are under stronger pressure to use this food in order to regain survival.

Maternal manipulation

To capture all components of selection on the traits in the model, it is enough to monitor four classes of individuals. They are: (1) young mothers, who produce first-brood offspring; (2) old mothers, who produce second-brood offspring; (3) first-brood subjects (or just subjects), who are the subset of first-brood offspring that the mother can choose to influence (e.g., they can be female offspring as for hymenopteran eusociality, or both female and male offspring as for isopteran eusociality); and (4) second-brood offspring. These four classes are respectively indexed by $i = \mathrm{m}, \mathrm{M}, 1, 2$.

A focal young mother influences a first-brood subject with probability p_{m} to delay dispersal from its natal nest. Here I make use of a notation that I will use throughout: for each trait, the first subscript indicates the class of the individual that controls the trait, while the trait without a class subscript refers to the population average trait value (Table 1). An influenced subject resists with probability q_1 and leaves its natal nest without delay. Alternatively, an influenced subject acquiesces with probability $1 - q_1$ and stays in its natal nest for some portion of its adulthood. An acquiescing subject expresses parental care (i.e., provisioning) while in its natal nest with some probability (the evolution of this probability

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is studied elsewhere; González-Forero, 2014). As stated above, this parental care is directed toward the available brood which are second-brood offspring. The survival of a second-brood offspring that was previously maternally provisioned increases by an amount b_{p} for each helper that helps it individually. In contrast, the survival of a second-brood offspring that was maternally neglected increases by an amount b_{n} for each helper that helps it individually. Such b_{p} and b_{n} specify the benefit from being helped. From the assumption that maternally neglected offspring use help more efficiently than maternally provisioned offspring, I assume that $b_{\mathrm{n}} > b_{\mathrm{p}}$. An increasing number of helpers increases the actual benefit received by helped offspring. Each helper splits uniformly its provisioning effort across second-brood offspring; thus, an increasing number of second-brood offspring decreases the actual benefit received by helped offspring (Charlesworth, 1978). The survival of a helper, which is the probability that the helper becomes a parent itself, decreases by c_{p} or c_{n} for helping maternally provisioned or maternally neglected offspring respectively. So, c_{p} and c_{n} define the costs of acquiescence which include the effect of missed reproductive opportunities due to delayed dispersal. Different costs of acquiescence for helping maternally provisioned or maternally neglected offspring $(c_{\mathrm{p}}, c_{\mathrm{n}})$ are introduced to allow for the fact that, if maternally neglected offspring are more demanding of food, it may be the case that $c_{\mathrm{n}} > c_{\mathrm{p}}$. Importantly, I assume that maternal influence and offspring resistance are costless (the effect of their costs is explored elsewhere; González-Forero and Gavrilets, 2013, González-Forero, 2014).

Resource allocation

I model maternal resource allocation as follows. After recently mated females compete globally for patches, each successful female secures a patch with resources. Of these

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resources, the female uses an amount of resource R in energy units to produce and to provision both first-brood subjects and second-brood offspring. The young mother allocates a fraction a_{m} of resource R to first-brood subjects, and the remaining fraction to the second brood. Of the resource allocated to first-brood subjects, the mother allocates a fraction e_{m1} into producing the offspring while she allocates the rest into provisioning them. Similarly, of the resource allocated to the second-brood, the mother allocates a fraction e_{m2} into producing the offspring and the rest into provisioning them (writing e_{m2} instead of e_{M2} makes no difference because it is the same mother that controls the trait). The energetic cost of producing an average offspring is γ_π and that of provisioning it is γ_{p}. For simplicity, I assume that the mother produces a continuous rather than a discrete number of offspring. Hence, the number of offspring of class $i = 1,2$ produced by the mother are respectively

$$n_1 = \frac{a_{\mathrm{m}} e_{\mathrm{m1}} R}{\gamma_\pi} \tag{1a}$$

$$n_2 = \frac{(1-a_{\mathrm{m}}) e_{\mathrm{m2}} R}{\gamma_\pi}. \tag{1b}$$

Thus, the total number of monitored offspring produced by a mother is $n = n_1 + n_2 = (R/\gamma_\pi)[a_{\mathrm{m}} e_{\mathrm{m1}} + (1-a_{\mathrm{m}}) e_{\mathrm{m2}}]$. The fraction of monitored offspring that are produced as first-brood subjects is $\alpha = n_1/n = a_{\mathrm{m}} e_{\mathrm{m1}}/[a_{\mathrm{m}} e_{\mathrm{m1}} + (1-a_{\mathrm{m}}) e_{\mathrm{m2}}]$. Now, the number of offspring of class $i = 1,2$ that the mother provisions herself is

$$n_{\mathrm{p1}} = \frac{a_{\mathrm{m}}(1-e_{\mathrm{m1}}) R}{\gamma_{\mathrm{p}}} \tag{2a}$$

$$n_{\mathrm{p2}} = \frac{(1-a_{\mathrm{m}})(1-e_{\mathrm{m2}}) R}{\gamma_{\mathrm{p}}}. \tag{2b}$$

Since the number of maternally provisioned offspring cannot be greater than the number of offspring ($n_{\mathrm{p}i} \leq n_i$), allocation to offspring production has by definition a lower bound given by $e_{\mathrm{m}i} \geq \gamma_\pi/(\gamma_\pi + \gamma_{\mathrm{p}})$, provided that the mother invests in the two broods (i.e.,

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$0 < a_{\mathrm{m}} < 1$).

In the model, the benefit received by helped offspring (b_{p}, b_{n}) and the cost of acquiescence paid by helpers (c_{p}, c_{n}) depend on the condition of the helped offspring (i.e., maternally provisioned or maternally neglected). Hence, for a focal helper, the average benefit and cost across its helped recipients depend on maternal resource allocation. Provided that the mother produces the two broods (so $0 < a_{\mathrm{m}} < 1$), the probability that a class-i offspring is maternally provisioned is $\zeta_i = n_{\mathrm{p}i}/n_i = (\gamma_\pi/\gamma_{\mathrm{p}})(1-e_{\mathrm{m}i})/e_{\mathrm{m}i}$. Then, for a focal helper, the average cost of acquiescence and the average benefit for its helped recipients are

$$c = c_{\mathrm{p}}\zeta_2 + c_{\mathrm{n}}(1-\zeta_2) \tag{3a}$$

$$b = b_{\mathrm{p}}\zeta_2 + b_{\mathrm{n}}(1-\zeta_2). \tag{3b}$$

Note that the benefit b and cost c are under maternal genetic control because they are functions of maternal allocation to offspring production ($e_{\mathrm{m}i}$) and provisioning ($1-e_{\mathrm{m}i}$).

Model implementation

I study the coevolution of the population average maternal influence (p), offspring costless resistance (q), and maternal resource allocation (a, e_1, e_2). I assume them to be additive, uncorrelated, quantitative genetic traits. The population is finite, reproduction is sexual and deterministic so genetic drift is ignored, and the genetic system is diploid or haplodiploid. The total resource in the environment measured in energy units is constant and is divided uniformly among successfully competing recently mated females, which regulates population growth. I use the approach of Taylor and Frank (1996) to obtain differential equations describing evolutionary change. This approach requires differentiation, so in order to apply it, I use conservative approximations of offspring

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survival to make offspring survival always differentiable. The mathematical details of the model are given in the Appendix. Additional notation is summarized in Table 2.

I solve numerically the differential equations describing evolutionary change. To properly initialize the numerical solutions, I first let maternal resource allocation evolve at a fast pace without genetic variation for manipulation or resistance during 1000 generations so that maternal resource allocation settles at an equilibrium. Then, I introduce genetic variation for manipulation and resistance. Supporting Figs. referenced below are in the Supporting Information 1 (SI1). The computer code used to generate all figures is in the Supporting Information 2 and 3 (SI2 and SI3).

Results

The coevolution of maternal influence (p), offspring costless resistance (q), and maternal resource allocation (a, e_1, e_2) yields the following result. At the start of the evolutionary process, both maternal influence and offspring resistance evolve (lines on red shade of Fig. 2a). Hence, there is a mother-offspring conflict over offspring helping behavior (red shade on Fig. 2a-f), and so maternal influence constitutes maternal manipulation during this stage. Manipulation produces a few helpers while resistance is still ineffective (green line on red shade of Fig. 2b). With help available, the mother reduces her maternal care toward second-brood offspring (red line on red shade of Fig. 2c). Thus, first-brood helpers help an increasing proportion of maternally neglected second-brood offspring (ζ_2 decreases from 1). Since by assumption maternally neglected offspring use help more efficiently, the average benefit received by second-brood offspring increases [blue line in Fig. 2d; see eq. (3b)]. The average benefit reaches a sufficiently high level that resistance becomes disfavored [non-shaded area in Fig. 2a; see eq. (A10b)]. Because there are no costs of

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resistance, resistance being disfavored means that the mother-offspring conflict disappears and maternal influence stops being maternal manipulation as defined above. First-brood subjects become effectively sterile because the cost for helping maternally neglected offspring is here maximal ($c_n = s_0$) and so the probability that first-brood subjects become parents (i.e., their survival to parenthood) evolves to zero (Fig. 2e). Daughters that successfully become mothers shift to being raised by sterile workers (Fig. 2f). At the end of this coevolutionary process, there is reproductive division of labor where reproductives (i.e., non-sterile offspring, which are the second brood) are produced by the mother but raised by workers (Fig. 2b,c,e), workers do not reproduce (Fig. 2e), and workers are maternally induced to help but are not selected to resist (Fig. 2a). Because of the final lack of conflict, the final maternal influence fits the notion of maternal signaling in the sense that it is a non-conflicting influence that evolved for the purpose of altering offspring's phenotype and offspring have evolved to attend to it (Maynard Smith and Harper, 2003). Therefore, despite there being no costs involved with resistance, maternal manipulation generates stable eusociality and an associated maternal signal that induces offspring to be workers. This process occurs both in haplodiploids and diploids (Supporting Figs. 3-5).

To assess whether the above process is likely to yield eusociality, I compare the model with two extreme possibilities in which either the mother or the offspring are in full control of offspring's helping behavior. For the first extreme possibility, I set both the initial resistance to maternal influence and the genetic variation for resistance to zero. I refer to this case as maternal control (MC). For the second extreme possibility, I use an otherwise analogous model except that staying in the natal nest is only under offspring control rather than being influenced by the mother (see Offspring control in Appendix). I refer to this case as offspring control (OC). I refer to the intermediate case where maternal influence and

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offspring resistance coevolve as shared control (SH). Under the specific parameter values used above for shared control (Fig. 2a-f), eusociality fails to evolve with offspring control (Fig. 2g-l and Supporting Figs. 6,7). Systematic exploration of the parameter space shows that the parameter region in which stable eusociality is obtained is consistently largest with maternal control, followed by shared control, and smallest with offspring control (Fig. 3 and Supporting Figs. 9-14). This result contrasts with previous understanding indicating that the parameter region for stable eusociality should be identical for shared control and offspring control when there are no direct costs associated with resistance (e.g., Craig, 1979, Keller and Nonacs, 1993, Cant, 2006, Uller and Pen, 2011). Specifically, stable eusociality can be obtained under smaller benefit-cost ratios with shared control than with offspring control when resistance to the maternal influence is entirely costless (note that b_{p} and c_{p} give the initial benefit and cost for helping because mothers initially provision all their offspring). This occurs more markedly when (1) maternally neglected offspring are substantially more efficient users of help than maternally provisioned offspring (i.e., $b_{\mathrm{n}} \gg b_{\mathrm{p}}$), and (2) the survival of maternally provisioned offspring can increase only moderately by being helped (i.e., $s_0 \rightarrow s_{\mathrm{max}}$; see Figs. 3a,b and Supporting Figs. 11a,b and 13a,b). More precisely, the latter condition states that the survival of maternally provisioned offspring must be close to saturation, which occurs when their survival if not helped (s_0) is already close to the maximum s_{max} they can have if helped.

Discussion

In eusocial taxa, queens exert substantial influence on their colonies by prompting offspring to develop or maintain worker phenotypes (e.g., Wilson, 1971, Fletcher and Ross, 1985, O'Donnell, 1998, Le Conte and Hefetz, 2008, Van Oystaeyen *et al.*, 2014). This

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maternal influence has suggested that maternal manipulation may have a role in the origin of eusociality (Alexander, 1974, Michener and Brothers, 1974, Linksvayer and Wade, 2005, Russell and Lummaa, 2009). A widespread mechanism by which queens influence their offspring is via pheromones (e.g., Le Conte and Hefetz, 2008, Van Oystaeyen *et al.*, 2014). However, if mothers manipulate offspring to help via pheromones, resistance to such manipulation could be rather costless and would freely evolve which suggests that eusociality created via manipulative pheromones would be evolutionarily unstable (Trivers, 1974, Craig, 1979, Keller and Nonacs, 1993). In contrast to this expectation, the results presented here show that maternal manipulation can yield stable eusociality when resistance to manipulation is costless. The reason is maternal care reduction provided that maternally neglected offspring use help more efficiently than maternally provisioned offspring. This reason is explained as follows.

Why can eusociality via maternal manipulation be stable when resistance is costless

When maternal manipulation starts evolving and resistance is still ineffective, the mother has some helpers that allow her to reduce maternal care toward the helped offspring and redirect the freed resources to produce additional offspring. If maternally neglected offspring use help more efficiently than maternally provisioned offspring to regain survival, then they benefit substantially more from the help. In consequence, as maternal care to helped offspring decreases, the benefit that helped offspring receive increases. The benefit can increase sufficiently that Hamilton's rule for helping becomes satisfied which eliminates selection for resistance [Hamilton, 1964; see eq. (A10b)]. Resistance is rendered disfavored because first- and second-brood offspring are siblings (in particular, full siblings

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for the parameters explored here). Given a mathematical equivalence between kin and group selection (Frank, 2012), one can interpret resistance as becoming disfavored once the benefit is large enough that kin or group selection start favoring acquiescence to the maternal influence.

Yet, in the model, acquiescence becomes favored because of maternal care reduction but not because of maternal fertility increase. There are two reasons for this. First, maternal fertility remains largely constant because maternal resource decreases due to population growth. There is a trade-off between offspring production and provisioning [defined by $e_{\mathrm{m}i}$ in eqs. (1) and (2)], so reduction in offspring provisioning releases maternal resources for offspring production (see Savage *et al.*, 2015 and Kramer *et al.*, 2015). However, the resource each mother secures is obtained from environmental resource divided among mothers so it depends on population size. The population grows once the mother starts to reduce care to second-brood offspring to produce more of them since their survival is high due to helping (Supporting Fig. 4i). Then, maternal resource becomes smaller with population growth which limits the ability of the mother to increase her fertility. Consequently, the number of second-brood offspring n_2 remains largely constant (Supporting Fig. 4f) because maternal resource R decreases with an increasing population size (Supporting Fig. 4n), while the number of maternally provisioned second-brood offspring $n_{2\mathrm{p}}$ decreases to zero (Supporting Fig. 4h). For example, suppose that at an early generation a manipulating mother with helpers secures resource that allows her to produce 10 second-brood offspring and provision all of them. Thanks to helping, in the next generation she produces 11 second-brood offspring and provisions 9 of them. The 11 second-brood offspring have high survival due to helping and the population grows. Then, a mother in the next generation has less resource. So, she can still produce 11 second-brood offspring even though she now

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provisions 8 of them. As a result, fertility increases little even if maternal care decreases. Therefore, although the benefit b can increase as the number of second-brood offspring increases, the observed increase in the benefit b is primarily due to maternal care reduction. This effect of competition would not easily be captured by assuming an infinite or constant population size or by imposing a carrying capacity.

Second, the benefit b that brings Hamilton's rule for helping to satisfaction [eq. (A10b)] is not a fertility benefit to the mother and is not weighted by relatedness to the mother. Instead, this benefit b is a survival benefit to siblings and is weighted by relatedness to siblings. In the model, helpers do not directly increase maternal fertility. To see this, note that, from eqs. (1), maternal fertility f_i is constant with respect to offspring resistance q_1. Helpers affect maternal fertility only indirectly by allowing the mother to decrease maternal care and redirect the freed resources into additional offspring production. Thus, a helper here does not directly increase maternal fertility because that depends on whether the mother chooses to use the help to reduce maternal care to increase her fertility. Because this choice is here controlled entirely genetically, the mother can only change her choice as the genes for the new choice spread. So, selection is unable to favor acquiescence due to increased maternal fertility if the fertility benefits to the mother occur only generations later. Now, helpers could directly help maternal fertility if they provisioned the mother thus giving her additional resource for offspring production (e.g., if maternal resource R were a function of offspring resistance q_1). However, in some species, provisioning the mother could demand a greater effect of the maternal influence than just causing offspring to stay as adults. This is because helpers would have to provision an adult rather than a young which may require additional changes to the normal behavioral repertoire of the offspring in some species (Hunt, 2007). Nevertheless, in species where

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provisioning the mother is a justified assumption (Wcislo and Gonzalez, 2006), an important extension of the model is to allow for this. Such an extension could allow for a marked increase in maternal fertility, which is not recovered in the model (Fig. 2b,c and Supporting Fig. 4f), probably because maternal resource R is limited to what the mother is able to find herself. For now, in the present model, acquiescence does not become favored because the mother becomes increasingly fertile. Instead, acquiescence becomes favored because the mother decreases maternal care. This highlights the importance of detailing how helping occurs and so who the direct recipient of the helping act is: in this model, it is second-brood offspring rather than the mother.

Conflict resolution because of the evolution of the benefit

The process reported here allows maternal manipulation to generate stable eusociality under smaller benefit-cost ratios than under offspring control despite resistance to manipulation being entirely costless (Fig. 3 and Supporting Figs. 9-14). As has been long established, if the mother has full control of offspring helping behavior, eusociality evolves under particularly small benefit-cost ratios (e.g., Charlesworth, 1978, Kapheim *et al.*, 2015; eusociality with MC in Fig. 3). The benefit-cost ratios where eusociality evolves are larger if offspring entirely control their helping behavior (e.g., Charlesworth, 1978, Kapheim *et al.*, 2015; eusociality with OC in Fig. 3). The region of disagreement where the mother favors offspring helping but offspring are not favored to help defines the battleground of the mother-offspring conflict (Godfray, 1995, Cant, 2006). Previous understanding indicates that if the control of offspring helping behavior is shared between mother and offspring and if offspring are not coerced in any way, stable eusociality would only evolve if offspring agree to helping in the first place (e.g., Craig, 1979, Keller and Nonacs, 1993, Cant, 2006,

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Uller and Pen, 2011). This understanding has suggested that when offspring are not coerced, considering offspring control should be sufficient to explain the evolution of offspring helping behavior (Trivers and Hare, 1976, Craig, 1979, Cant, 2006, Uller and Pen, 2011, Kuijper and Hoyle, 2015). Contrary to this understanding, the results obtained here show that some of the advantage of maternal manipulation to generate eusociality can be maintained even if resistance to manipulation is costless. The reason is that with maternal manipulation, an initially moderate benefit that disfavors helping can evolve and increase sufficiently that helping becomes favored: the mother can produce ineffectively resisting helpers that allow her to reduce maternal care, thereby increasing the benefit and stabilizing eusociality. In contrast, without maternal manipulation, a moderate benefit that disfavors helping does not increase to favor helping: the mother does not have helpers, and since she does not have helpers she does not evolve reduced maternal care that would allow the benefit to increase.

Hence, the evolution of the benefit eliminates the mother-offspring conflict introduced by manipulation. This is consistent with a previous study where the evolution of the benefit also eliminates the mother-offspring conflict (González-Forero, 2014). In that study, the benefit is genetically controlled by the helper because the helper controls its helping efficiency. In contrast, here the benefit is genetically controlled by the mother because she controls offspring condition by controlling whether an offspring is provisioned or not, which determines offspring efficiency of help use [see eq. (3b)].

After the mother-offspring conflict disappears, the maternal influence fits the notion of a signal in the sense that it is a non-conflicting influence that evolved for the purpose of altering offspring's phenotype while offspring's response also evolved to attend to it (Maynard Smith and Harper, 2003). The resulting signal only informs first-brood offspring

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of the brood they belong to and in principle could be maintained in evolutionary time to prevent second-brood offspring from staying to help a non-existent third brood (González-Forero, 2014). Given the final absence of mother-offspring conflict over offspring helping behavior, mother and offspring could then evolve in a mutually beneficial way. Mutually beneficial coevolution would allow for subsequent elaborations of the maternal signal. If offspring evolve the ability to provision their mother, offspring could become more sensitive to maternal fertility since they affect it directly (see above for why directly helping their mother is important for maternal fertility to affect selection for helping). Then, the maternal signal could in principle evolve into an honest signal of queen fertility. This pathway would link the origin of eusociality to the evidence suggesting that queen pheromones act as honest signaling of the queen's reproductive health (Heinze and d'Ettorre, 2009, van Zweden *et al.*, 2014).

The assumption of efficient help use

The model assumes that maternally neglected offspring use help more efficiently than maternally provisioned offspring. This assumption relies on the expectation that maternally neglected offspring can be under strong pressure to regain survival relative to maternally provisioned offspring. This assumption can be tested by constructing regression lines for the survival of maternally provisioned and maternally neglected offspring vs. the ratio of the number of helpers to recipients of help. The assumption states that the slope for maternally neglected offspring is larger than for maternally provisioned offspring when the ratio of the number of helpers to recipients approaches zero (see Supporting Figs. 1 and 2).

The more efficient help use by maternally neglected offspring refers to their physical

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ability to do so. It does not refer to the mathematical consequence that the marginal survival benefit they receive from being helped is necessarily larger than that obtained by maternally provisioned offspring. Indeed, maternally neglected offspring die if not helped and their asymptotic survival with an increasing number of helpers is here the same as for maternally provisioned offspring. It can then be checked that, for the differentiable approximations of survival used, the marginal benefit to maternally neglected offspring (which is the negative of the derivative of s_2 with respect to Q setting $\zeta_2 = 0$) is larger than that of maternally provisioned offspring even if $b_\mathrm{n} = b_\mathrm{p}$. However, such larger marginal benefit is not enough to eliminate the mother-offspring conflict if $b_\mathrm{n} = b_\mathrm{p}$ (results not shown). Instead, the physical efficiency of help use must be larger for maternally neglected offspring ($b_\mathrm{n} > b_\mathrm{p}$). This physical ability can be assessed as described in the previous paragraph.

Model predictions

When the assumption of efficient help use by maternally neglected offspring holds, the model makes predictions to discern whether eusociality where ignoring maternal influence is rather costless is likely to have originated from maternal manipulation rather than from offspring control. For one prediction, two quantities must be estimated: baseline offspring survival (s_0) and maximum offspring survival (s_max). These two quantities can be estimated from the probability that maternally provisioned offspring become parents when not helped (s_0) and when helped by a large number of helpers (s_max). A testable prediction is that the survival of maternally provisioned offspring should be close to saturation (s_0 approaches s_max) in the eusocial species under consideration (Fig. 3a,b and Supporting Figs. 11a,b and 13a,b). This prediction allows to disentangle manipulation and offspring

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control as sources of eusociality because eusociality via offspring control is not more likely when the survival of maternally provisioned offspring is close to saturation (Fig. 3 and Supporting Figs. 9-14).

The disappearance of the mother-offspring conflict also predicts the occurrence of "conflict relics". By a conflict relic I mean a trait that ancestrally served as an adaptation for manipulation or resistance but lost this function. Conflict relics can be morphological, molecular, or behavioral. For example, conflict relics might be involved in the following phenomenon. In the ants *Diacamma*, queens have been secondarily lost but eusociality remains and only one worker (gamergate) in the colony reproduces. Colonies reproduce by fission, which produces two colonies but one of them has no reproductive individuals. In this colony, the first emerging adult bites off the "gemmae" of subsequently emerging adults, rendering them unable to mate because gemmae are necessary for calling foreign males and mating (Fukumoto *et al.*, 1989, Peeters and Higashi, 1989, Nakata *et al.*, 1998). As a consequence, the first emerging adult becomes the only reproductive individual in the newly formed colony. However, in one population of *Diacamma*, gemma mutilation does not occur and instead the reproductive monopoly is established via dominance interactions. Interestingly, mutilation does not occur if brood of the non-mutilating population are raised by a mutilating colony (Ramaswamy *et al.*, 2004). On the contrary, mutilation occurs if brood of a mutilating population are raised by a non-mutilating colony. This has suggested that the brood itself produces the cues that cause them to be mutilated (Ramaswamy *et al.*, 2004). Moreover, behavioral conflict between the mutilating gamergate and its victims is largely absent when the gamergate is mature (Baratte *et al.*, 2006). If evidence is found suggesting that cues originating in the mutilated individuals are in addition evolved signals to be mutilated, this would suggest that mutilation is a conflict

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relic. In this example, resistance to mutilation is costly or unavailable, so other models of conflict resolution apply (Baratte *et al.*, 2006, Ratnieks *et al.*, 2006). Nonetheless, in other cases where resistance is available and rather costless, as is thought to be the case for queen pheromones (Keller and Nonacs, 1993), the model here predicts the occurrence of conflict relics. Because conflict relics are not predicted if eusociality originates via offspring control, conflict relics also allow to disentangle manipulation and offspring control as a source of eusociality, specifically when the maternal influence is rather costless to ignore.

Technicalities of biological importance

When the costs and benefits of the helping behavior are fertility costs and benefits, helping is known to be favored when helpers have lower reproductive value than helped individuals (West Eberhard, 1975, Frank, 1998), which has prompted hypotheses for the evolution of eusociality (e.g., Holman, 2014). In the model presented here, the costs and benefits of the helping behavior are only survival costs and benefits, and so it is the class equilibrium frequency (u_i) rather than reproductive values that can change the direction of selection for acquiescence [the derivatives of f_i in eqs. (A9) are here zero]. Calculation of class equilibrium frequencies (see Demographic variables in Appendix) shows that they can only change the direction of selection via the sex ratio in the two broods [i.e., the $\eta_j \sigma_j$ occurring in r_{ji} in eqs. (A10)], which I assumed even and constant. Yet, in the model, first-brood individuals evolve low reproductive values as their survival decreases, while second-brood individuals evolve high reproductive values as their survival increases [eqs. (A16c) and (A16d) and Supporting Figs. 2l and 3l], which matches the expected pattern.

The model considers a finite population where population size is regulated in a relatively natural way. No carrying capacity is imposed but arises from the finite

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environmental resource. Thus, population size and the number of individuals of different classes can be tracked through time (Supporting Figs. 2i,j and 3i,j). Although the model's complexity prevents analytical treatment, a simpler version of the model suggests that a necessary condition for stable eusociality via the process reported here is a condition of the form $br + (1 - q_0)A > c$ so that acquiescence can become favored as the benefit evolves (see eq. A3.50e in González-Forero, 2013). In this inequality, r is relatedness of first- to second-brood offspring, q_0 is the initial resistance, and A is proportional to the ratio of the genetic variances of maternally controlled traits over the genetic variance of offspring resistance. This suggests that large genetic variances for maternally controlled traits relative to offspring controlled traits would favor the disappearance of conflict via this process. Regarding interpretation, the model described parental care as provisioning, but it can be equivalently taken as nest defense provided that defense is directed to individuals rather than to the whole brood (Cocroft, 2002). Parental care in the form of defense is important because nest defense is thought to have been key for the origin of isopteran eusociality (Korb *et al.*, 2012). In this interpretation of the model, reduced maternal care toward second-brood offspring refers to reduced maternal investment into defending individual second-brood offspring.

Finally, two underlying assumptions of the models are important regarding the role of maternal influence in the high incidence of eusociality in hymenoptera. In the offspring control model, only first-brood offspring express the genes to stay without maternal influence. This implicitly assumes that a gene for helping has a dual function: detecting that it occurs in a first-brood individual rather than in a second-brood individual and triggering the expression of helping. In the shared control model, the corresponding dual function is for a gene controlling the maternal influence: detecting first-brood offspring

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and expressing the maternal influence toward them. The dual function for a helping gene can occur if non-helping first-brood individuals already use environmental cues that can trigger the helping gene expression. On the other hand, the dual function for the maternal influence gene may be particularly feasible in hymenoptera relative to other taxa. Hymenopteran mothers can control the sex of their offspring by fertilizing eggs (Verhulst *et al.*, 2010), and their first offspring are often female for many eusocial hymenopterans as well as for their solitary sister taxa (Hunt, 2007). The mother can then control which brood she is laying and of which sex those offspring are. Since in solitary hymenoptera parental care is typically only maternal (Lin and Michener, 1972), the dual ability for the maternal influence gene can then be translated into the more likely requirement that the gene is expressed early in the reproductive phase of a hymenopteran mother. In contrast, for diploids, early expression of the maternal influence gene would facilitate the dual gene function only if (1) the early brood is composed of a sex that provides parental care, or (2) the early brood is composed of the two sexes and there is biparental care, as is thought to be the case for isopteran ancestors (Klass *et al.*, 2008). These considerations rely on patterns of parental care and hymenopteran sex determination, rather than on parental care being more likely to evolve in haplodiploid systems which is another consideration that has not been supported by recent models (e.g., Wade, 2001, Linksvayer and Wade, 2005, Gardner, 2012, Davies and Gardner, 2014).

Conclusion

The joint action of maternal manipulation and maternal care reduction can generate stable eusociality even if resistance to manipulation is costless provided that maternally neglected offspring are highly efficient help users. This process offers a mechanism

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through which eusociality can arise from a population where only parental care is present if maternal manipulation can be executed and if it is initially favored.

Acknowledgments

I thank Sergey Gavrilets, Kelly Rooker, Jeremy Auerbach, Xavier Thibert-Plante, Laurent Lehmann, Charles Mullon, Simon Powers, Slimane Dridi, Matthias Wubs, Valeria Montano, Danielle Mersch, Laurent Keller, Luke Holman, and two anonymous reviewers for valuable discussion or comments on the manuscript at various stages of the project. I thank L. Holman who refereeing the manuscript suggested to keep the term manipulation for conflict situations to better agree with common usage of the concept. I thank S. Gavrilets for access to the Volos computer cluster where I ran numerical simulations conducive to the results reported here. I was funded by a Graduate Research Assistantship from the National Institute for Mathematical and Biological Synthesis (NIMBioS). NIMBioS is sponsored by the National Science Foundation, the U.S. Department of Homeland Security, and the U.S. Department of Agriculture through NSF Award # EF-0832858, with additional support from The University of Tennessee, Knoxville. Volos is funded by the NIH grant # GM-56693 to S. Gavrilets.

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Table 1: Notation for the traits.

In a focal individual	Population average	Definition
p_{m}	p	Probability that a mother influences first-brood subjects
q_1	q	Probability that an influenced subject resists the influence
a_{m}	a	Fraction of maternal resource allocated to first-brood subjects
$e_{\mathrm{m}1}$	e_1	Fraction of the allocated resource to first-brood subjects that the mother spends producing them (she spends the rest provisioning them)
$e_{\mathrm{m}2}$	e_2	Fraction of the allocated resource to second-brood offspring that the mother spends producing them
x_1	x	Probability that a first-brood subject stays spontaneously

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Table 2: Additional notation. Offspring condition is $k = \mathrm{p}, \mathrm{n}$ if maternally provisioned or maternally neglected.

b_k	Survival benefit received by a helped offspring in condition k
b	Average benefit received by helped offspring
d	Extent to which b_p and b_n are similar
c_k	Survival cost paid for helping a sibling in condition k
c	Average cost for helping siblings
E	Total environmental resource
R	Resource per mother
$\gamma_\pi, \gamma_\mathrm{p}$	Energetic cost of producing and provisioning an average offspring
n_i	Number of class-i offspring produced
f_i	Number of class-i offspring produced weighted by maternal genetic contribution
$n_{\mathrm{p}i}$	Number of class-i offspring that are maternally provisioned
ζ_i	Fraction of class-i offspring that are maternally provisioned
s_0	Baseline probability that an offspring becomes a parent
s_max	Maximum probability that a helped offspring becomes a parent
s_m	Probability that a young mother survives to become an old mother
s_1, s_2	Probability that a 1st-brood subject or 2nd-brood offspring becomes a mother
s_{2k}	Probability that a helped 2nd-brood offspring in condition k becomes a parent
η_i	Average genetic contribution of a mother to class-i offspring
$\theta_♀, \theta_♂$	Genetic contribution of a mother to female or male offspring
σ_i	Proportion of female offspring produced in class-i offspring
N_i	Number of class-i individuals in the population
u_i	Ecological equilibrium frequency of class-i individuals in the population
v_i	Reproductive value of class-i individuals
ρ_{ji}	Regression relatedness of an average class-i actor toward an average class-j recipient
r_{ji}	Weighted regression relatedness, $\eta_j \sigma_j \rho_{ji}$
V_z	Additive genetic variance of trait z
g_z	Breeding value (additive genetic component) of trait z in the actor

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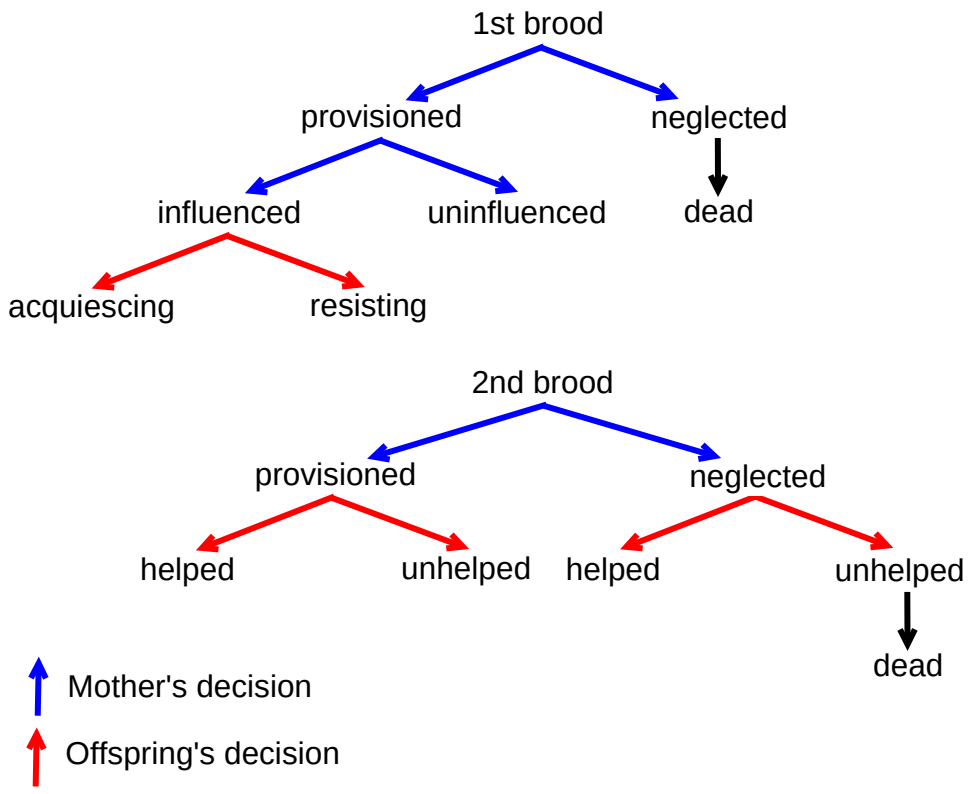

Figure 1: Tree description of the model. See text for details.

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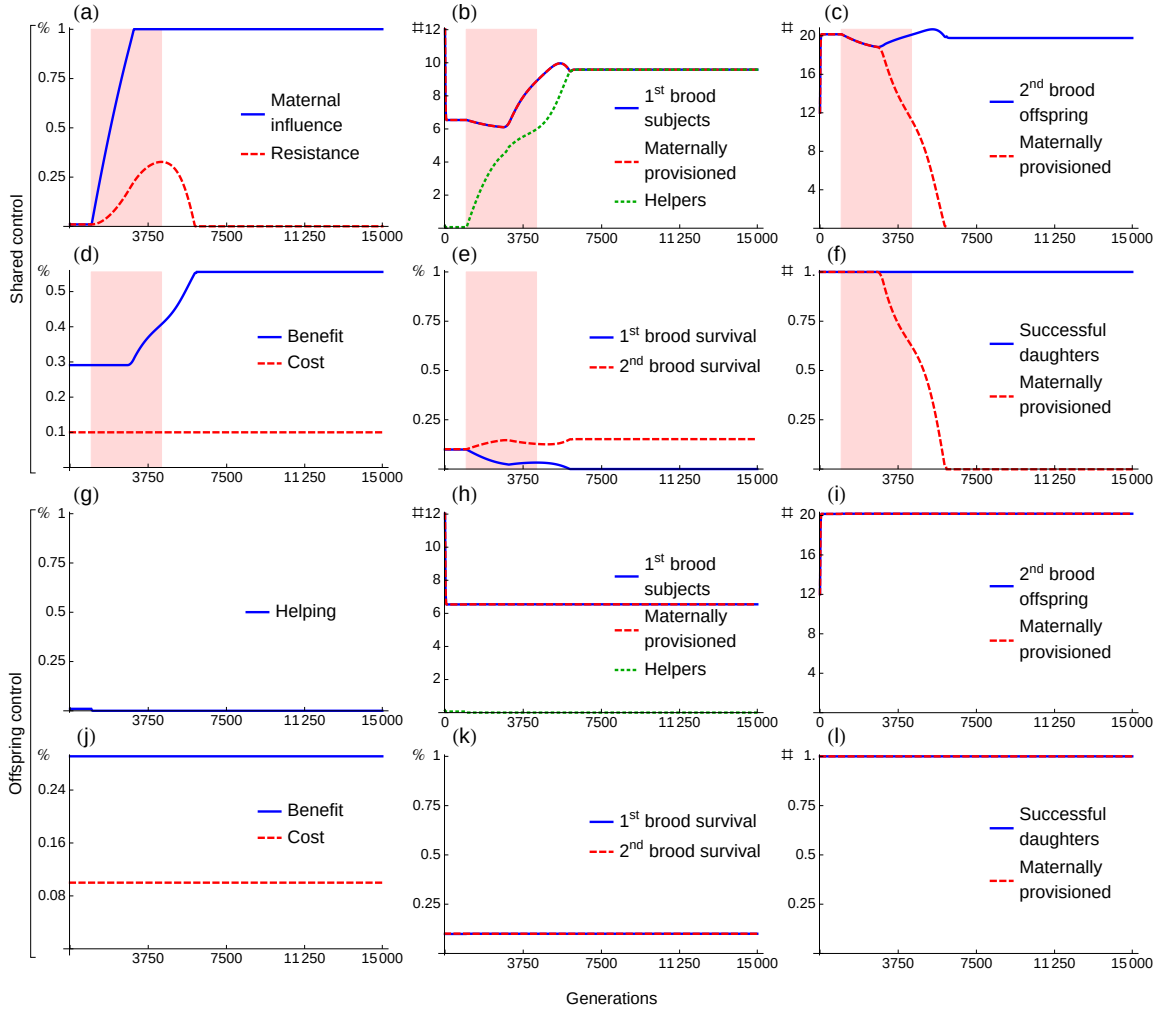

Figure 2: Stable eusociality via maternal manipulation with costless resistance. The plots show population-average values vs. generations. In the two top rows, offspring can be influenced by their mother to stay to help (shared control) (a-f). In the two bottom rows, offspring can stay without being influenced (offspring control) (g-l). In red shades, resistance to the maternal influence is favored to evolve (mother-offspring conflict). Because (a) resistance is initially ineffective, (b) the mother initially has some helpers that (c) allow her to reduce maternal care to the second brood, thereby (d) increasing the benefit that second-brood offspring receive from being helped which (a) eliminates selection for resistance. The genetic system is haplodiploid. Parameter values are in the Supporting Information 1 (SI1).

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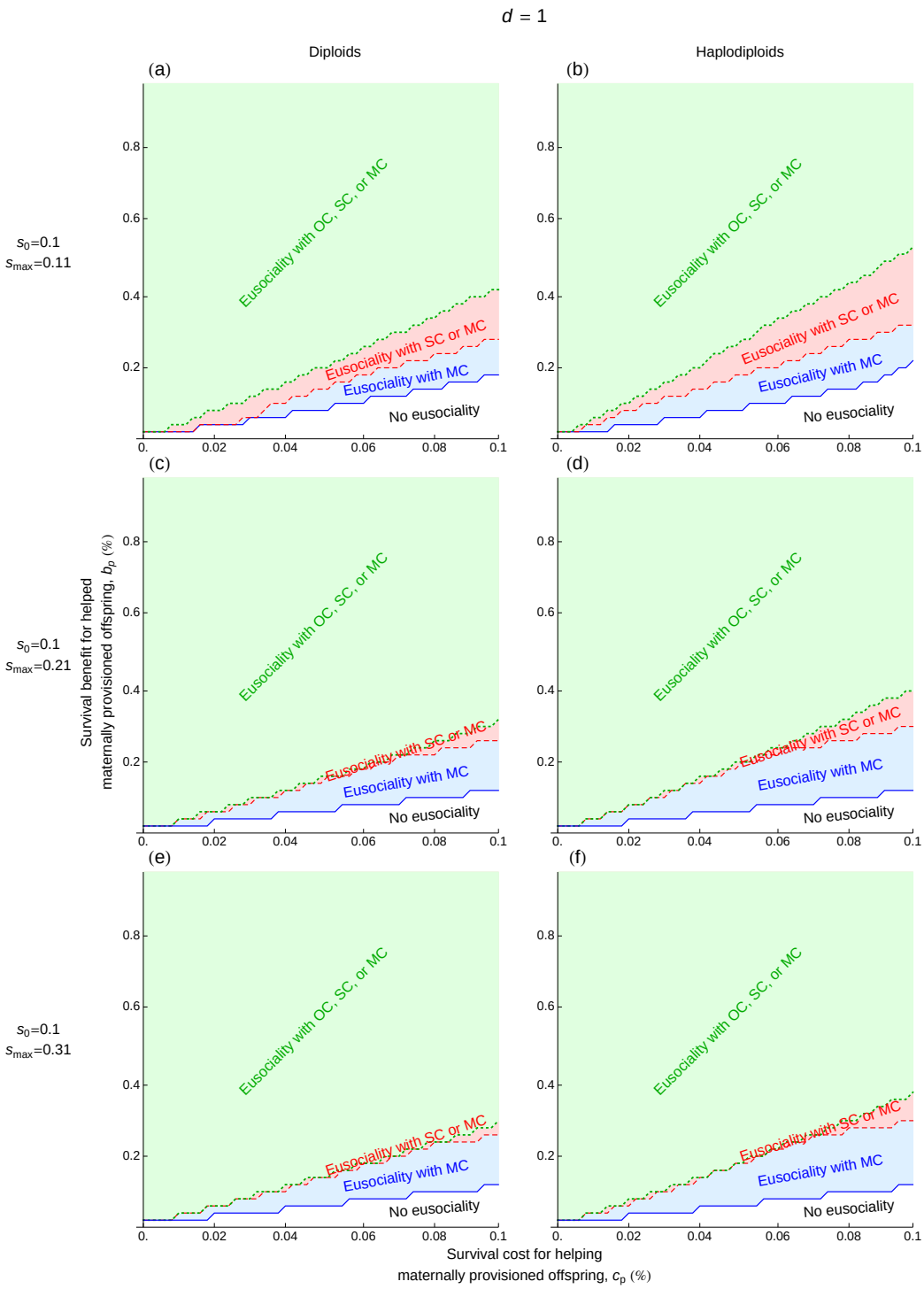

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Figure 3: Stable eusociality via maternal manipulation can be obtained under smaller benefit-cost ratios than via offspring control despite costless resistance. The graphs show the outcome across values of the survival benefit for helped maternally provisioned offspring (b_{p}) vs. the survival cost for helping maternally provisioned offspring (c_{p}). In blue shade, eusociality is obtained with maternal control of offspring helping behavior (MC). In red shade, eusociality is obtained with either shared control (SC) or maternal control (MC). In green shade, eusociality is obtained with either offspring control (OC), shared control (SC), or maternal control (MC). When the cost for helping maternally provisioned siblings is maximal (here $c_{\mathrm{p}} = s_0 = 0.1$), the initial workers are sterile. An evolutionary outcome was considered eusociality if at the end of the process the two broods were present ($n_i \geq 1$) and if there was at least one sterile helper in the first brood [$n_{\mathrm{p1}}\, p(1-q) \geq 1$; sterility occurs because in all panels $c_{\mathrm{n}} = s_0 = 0.1$]. For the left column, the genetic system is diploid (a,c,e). For the right column, the genetic system is haplodiploid (b,d,f). In all panels, $s_0 = 0.1$. For the top row, $s_{\mathrm{max}} = 0.11$ (a,b), the middle row $s_{\mathrm{max}} = 0.21$ (c,d) and the bottom row $s_{\mathrm{max}} = 0.31$ (e,f). Finally, $b_{\mathrm{n}} = b_p d\, s_{\mathrm{max}}/(d\, s_{\mathrm{max}} - s_0)$ and $d = 1$. The remaining parameter values are in the SI1.

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Appendix

Life history implementation

I separate time into ecological and evolutionary scales. Individuals reproduce in an ecological time scale, and traits change in an evolutionary time scale. I assume that the ecological time scale is much faster than the evolutionary one. Ecological time is discrete, while evolutionary time is continuous. At each ecological time, I monitor the defined four classes of individuals: young mothers, old mothers, first-brood subjects, and second-brood offspring (indexed by $i = \mathrm{m}, \mathrm{M}, 1, 2$). A mother produces n_i offspring of class i $(= 1, 2)$. A fraction σ_i of n_i is female. The average genetic contribution of the mother to class-i offspring is η_i $[= \sigma_i \theta_{♀} + (1 - \sigma_i)\theta_{♂}$, where θ_l is the genetic contribution of a mother to sex-l offspring; for diploids, $\theta_l = 1/2$, and for haplodiploids, $\theta_{♀} = 1/2$ while $\theta_{♂} = 1]$. Maternal fertility through class-i offspring is $f_i = \eta_i n_i$ (Taylor, 1990). Survival of class-i offspring $(i = 1, 2)$, defined as the probability that a class-i offspring becomes a young mother, is s_i. The probability that a young mother becomes an old mother is s_{m}. The number of class-i individuals in the population at ecological time τ is $N_i(\tau)$. With $\mathbf{N} = (N_{\mathrm{m}}, N_{\mathrm{M}}, N_1, N_2)^T$, then $\mathbf{N}(\tau + 1) = \mathbf{W}\mathbf{N}(\tau)$ where

$$\mathbf{W} = \begin{pmatrix} 0 & 0 & s_1 & s_2 \\ s_{\mathrm{m}} & 0 & 0 & 0 \\ f_1 & 0 & 0 & 0 \\ 0 & f_2 & 0 & 0 \end{pmatrix}. \tag{A1}$$

Survival

I assume that maternal survival s_{m} only depends on a constant environmental mortality, and so s_{m} is independent of the evolving traits. The probability that a maternally

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provisioned offspring becomes a parent in the absence of maternal influence or help is s_0 (baseline survival). Since survival s_i $(i = 1,2)$ is the probability of becoming a young mother, the survival of a first-brood subject (who is a female with probability σ_1) is

$$s_1 = \sigma_1 \left\{\zeta_1 \left[p_\mathrm{m}(1-q_1)(s_0 - c) + p_\mathrm{m} q_1 s_0 + (1-p_\mathrm{m}) s_0\right] + (1-\zeta_1) \times 0\right\} \tag{A2a}$$

$$= \sigma_1 \zeta_1 \left[s_0 - c p_\mathrm{m}(1-q_1)\right]. \tag{A2b}$$

The probability that a second-brood offspring in condition k $(k = \mathrm{p}, \mathrm{n})$ becomes a parent after being helped is s_{2k}. The average resistance probability among the first-brood subjects of a mother is Q. So, $p_\mathrm{m}(1-Q)$ is the probability that first-brood subjects are helpers. Then, the survival of a second-brood offspring is

$$s_2 = \sigma_2 \left\{\zeta_2 \left[p_\mathrm{m}(1-Q) s_{2\mathrm{p}} + p_\mathrm{m} Q s_0 + (1-p_\mathrm{m}) s_0\right]\right. \tag{A3a}$$

$$\left. + (1-\zeta_2)\left[p_\mathrm{m}(1-Q) s_{2\mathrm{n}} + p_\mathrm{m} Q \times 0 + (1-p_\mathrm{m}) \times 0\right]\right\} \tag{A3b}$$

$$= \sigma_2 \left\{s_0 \zeta_2 + p_\mathrm{m}(1-Q)\left[\zeta_2 (s_{2\mathrm{p}} - s_0) + (1-\zeta_2) s_{2\mathrm{n}}\right]\right\}. \tag{A3c}$$

To fully specify the survival of second-brood offspring (s_2), it remains to specify the survival of helped second-brood offspring in condition k (s_{2k}).

Let s_max be the maximum probability of becoming a parent after receiving help (maximum survival). Following Charlesworth (1978), the survival of maternally provisioned offspring after being helped is

$$s_{2\mathrm{p}} = \begin{cases} s_0 + b_\mathrm{p} \frac{n_{\mathrm{p}1}}{n_2} & \text{if } \frac{n_{\mathrm{p}1}}{n_2} \leq \frac{s_\mathrm{max} - s_0}{b_\mathrm{p}} \\ s_\mathrm{max} & \text{otherwise.} \end{cases} \tag{A4a}$$

The factor $n_{\mathrm{p}1}/n_2$ is the number of possible helpers over the number of recipients but since $s_{2\mathrm{p}}$ is already conditioned on the fact that the second-brood individual is helped, then $n_{\mathrm{p}1}$ here gives the number of actual helpers. Survival $s_{2\mathrm{p}}$ saturates to s_max if the ratio of helpers

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to recipients n_{p1}/n_2 is sufficiently large. The survival of maternally neglected offspring after being helped is

$$s_{2\mathrm{n}} = \begin{cases} 0 + b_{\mathrm{n}} \frac{n_{\mathrm{p1}}}{n_2} & \text{if } \frac{n_{\mathrm{p1}}}{n_2} \leq \frac{s_{\max}}{b_{\mathrm{n}}} \\ s_{\max} & \text{otherwise.} \end{cases} \tag{A4b}$$

When the ratio of helpers to recipients is sufficiently small $[n_{\mathrm{p1}}/n_2 \leq (s_{\max} - s_0)/b_{\mathrm{p}}, s_{\max}/b_{\mathrm{n}}]$, then the survival of a second-brood offspring reduces to

$$s_2 = \sigma_2 \left[s_0 \zeta_2 + b \frac{n_{\mathrm{p1}} p_{\mathrm{m}} (1-Q)}{n_2} \right]. \tag{A5}$$

Survival approximation

Survivals after being helped (s_{2k}) are not differentiable at their switching points when n_{p1}/n_2 becomes too large. The method of Taylor and Frank (1996) requires differentiation, so I approximate s_{2k} by always differentiable functions as follows. Denoting $\xi = n_{\mathrm{p1}}/n_2$, we can write $s_{2\mathrm{p}}$ as a function $s_{2\mathrm{p}}(\xi)$ which can be approximated from below by a function of the form

$$F(\xi) = A_1 [A_2 - \exp(-A_3 \xi)], \tag{A6}$$

for some A_1, A_2, A_3. Setting $F(0) = s_0$ and $F(\infty) = s_{\max}$, we find $A_1 = s_{\max} - s_0$ and $A_2 = s_{\max}/A_1$. Choosing $F'(0) = b_{\mathrm{p}}$, we obtain $A_3 = b_{\mathrm{p}}/A_1$. Proceeding similarly with $s_{2\mathrm{n}}$, we recover the approximations

$$s_{2\mathrm{p}} \approx s_{\max} - (s_{\max} - s_0) \exp\left[-b_{\mathrm{p}}/(s_{\max} - s_0)(n_{\mathrm{p1}}/n_2)\right] \tag{A7a}$$

$$s_{2\mathrm{n}} \approx s_{\max} \left\{1 - \exp\left[-b_{\mathrm{n}}/s_{\max}(n_{\mathrm{p1}}/n_2)\right]\right\}, \tag{A7b}$$

which hold for any $n_{\mathrm{p1}}/n_2 > 0$ (see Supporting Fig. 2).

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Population regulation

Young mothers compete globally for resources to produce and provision first-brood subjects and second-brood offspring. The environment has a constant amount E of resources in energy units that females use for these purposes. Environmental resource E is divided uniformly among young mothers, so each young mother has an amount of resource $R = E/N_{\mathrm{m}}$. I assume that the population reaches zero growth during ecological time, which occurs when the leading eigenvalue of $\mathbf{W}$ is one; that is, when $f_1 s_1 + s_{\mathrm{m}} f_2 s_2 = 1$ evaluated at population average values, which is a version of the Euler-Lotka equation (Charlesworth, 1994). Solving for N_{m} yields the ecologically stationary number of young mothers

$$N_{\mathrm{m}} = \frac{E}{\gamma_\pi}\left[\eta_1 a e_1 s_1 + \eta_2 (1-a) e_2 s_2 s_{\mathrm{m}}\right] \tag{A8}$$

evaluated at population averages. Population size is $N = N_{\mathrm{m}} + N_{\mathrm{M}} + N_1 + N_2$, where from $\mathbf{N} = \mathbf{WN}$ we have that $N_{\mathrm{M}} = s_{\mathrm{m}} N_{\mathrm{m}}$, $N_1 = f_1 N_{\mathrm{m}}$, and $N_2 = f_2 N_{\mathrm{M}}$. Notice that although population size remains constant in ecological time scales, it can evolve in evolutionary time scales as trait values change. From eqs. (1), it follows that the ecologically stationary number of offspring is $n = 1/\left[\eta_1 \alpha s_1 + \eta_2 (1-\alpha) s_2 s_{\mathrm{m}}\right]$.

Dynamic equations

I study the coevolution of maternal influence, resistance, and maternal resource allocation (i.e., p, q, a, e_1, and e_2, which denote population averages). As previously stated, I assume they are additive, uncorrelated, quantitative genetic traits. The additive genetic variance of trait z is V_z $(z = p, q, a, e_1, e_2)$. From the previous section, R is a function of population average trait values and is then constant with respect to the actor's breeding value (i.e., the additive genetic component of the trait in the individual controlling the trait). The equilibrium frequency of class-i individuals during the ecological time scale, or simply the

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class-i ecological equilibrium frequency, is u_i. The individual reproductive value of class-i individuals is v_i. u_i and v_i are respectively the right and left eigenvectors of $\mathbf{W}$ after normalization so that $\sum u_i = \sum u_i v_i = 1$ (Leslie, 1948, Taylor, 1990). I assume that mutation and selection are weak. Thus, for evolutionary time t, the change in the population average value of trait z can be approximated (Taylor and Frank, 1996, Frank, 1997) by

$$\frac{dz}{dt} = V_z \sum_{ij} v_i \frac{\partial w_{ij}}{\partial g_z} u_j \tag{A9a}$$

$$= V_z \left(v_\mathrm{m} \frac{\partial s_1}{\partial g_z} u_1 + v_\mathrm{m} \frac{\partial s_2}{\partial g_z} u_2 + v_1 \frac{\partial f_1}{\partial g_z} u_\mathrm{m} + v_2 \frac{\partial f_2}{\partial g_z} u_\mathrm{M} \right) \tag{A9b}$$

$$= \frac{1}{\Lambda} V_z \left(f_1 \frac{\partial s_1}{\partial g_z} + s_\mathrm{m} f_2 \frac{\partial s_2}{\partial g_z} + s_1 \frac{\partial f_1}{\partial g_z} + s_\mathrm{m} s_2 \frac{\partial f_2}{\partial g_z} \right), \tag{A9c}$$

evaluated at population averages, where w_{ij} is the ij-th entry of $\mathbf{W}$, g_z is the actor's breeding value for z, and $\Lambda = 2 + s_\mathrm{m} f_2 s_2$ is a scaling factor due to population growth. The values of u_i and v_i are found below in Demographic variables.

I solve system (A9) numerically making use of the approximations of s_{2k} in eqs. (A7) [see Supporting Information 3 (SI3) for computer code]. However, the exact s_{2k} yield a system that is conceptually useful. Specifically, for $n_{\mathrm{p}1}/n_2 \leq (s_\mathrm{max} - s_0)/b_\mathrm{p}, s_\mathrm{max}/b_\mathrm{n}$, using the exact s_{2k} yields

$$\frac{dp}{dt} = \frac{1}{\Lambda} V_p n_{\mathrm{p}1} (1-q)(b r_{2\mathrm{m}} s_\mathrm{m} - c r_{1\mathrm{m}}) \tag{A10a}$$

$$\frac{dq}{dt} = -\frac{1}{\Lambda} V_q n_{\mathrm{p}1} p (b r_{21} s_\mathrm{m} - c r_{11}) \tag{A10b}$$

$$\frac{da}{dt} = \frac{1}{\Lambda} V_a \frac{R}{\gamma_\mathrm{p}} \left\{ s_0 \left[(1-e_1) r_{1\mathrm{m}} - (1-e_2) r_{2\mathrm{m}} s_\mathrm{m} \right] + p(1-q)(1-e_1)(b r_{2\mathrm{m}} s_\mathrm{m} - c r_{1\mathrm{m}}) \right\} \tag{A10c}$$

$$\frac{de_1}{dt} = -\frac{1}{\Lambda} V_{e_1} a \frac{R}{\gamma_\mathrm{p}} \left[s_0 r_{1\mathrm{m}} + p(1-q)(b r_{2\mathrm{m}} s_\mathrm{m} - c r_{1\mathrm{m}}) \right] \tag{A10d}$$

$$\frac{de_2}{dt} = -\frac{1}{\Lambda} V_{e_2} (1-a) \frac{R}{\gamma_\mathrm{p}} \left\{ s_0 r_{2\mathrm{m}} s_\mathrm{m} - p(1-q) \frac{n_{\mathrm{p}1}}{n_2} \frac{1}{e_2} \left[(b_\mathrm{n} - b_\mathrm{p}) r_{2\mathrm{m}} s_\mathrm{m} - (c_\mathrm{n} - c_\mathrm{p}) r_{1\mathrm{m}} \right] \right\}. \tag{A10e}$$

where $r_{ji} = \eta_j \sigma_j \rho_{ji}$, $\rho_{ji} = dz_j / dg_{z_i}$ is the regression relatedness of class-i actor to class-j recipient, z_j is the trait in the recipient, and g_{z_i} is the breeding value in the actor (see SI2

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for check of the derivation).

No helping

By removing maternal influence (setting $p = 0$ and $V_p = 0$), system (A10) reduces to

$$\frac{da}{dt} = \frac{1}{\Lambda} V_a \frac{R}{\gamma_{\mathrm{p}}} s_0 \left[(1-e_1) r_{1\mathrm{m}} - (1-e_2) r_{2\mathrm{m}} s_{\mathrm{m}}\right] \tag{A11a}$$

$$\frac{de_1}{dt} = -\frac{1}{\Lambda} V_{e_1} a \frac{R}{\gamma_{\mathrm{p}}} s_0 r_{1\mathrm{m}} \tag{A11b}$$

$$\frac{de_2}{dt} = -\frac{1}{\Lambda} V_{e_2} (1-a) \frac{R}{\gamma_{\mathrm{p}}} s_0 r_{2\mathrm{m}} s_{\mathrm{m}}. \tag{A11c}$$

This system evolves to minimal investment in offspring production [i.e., $e_1^* = e_2^* = \gamma_\pi / (\gamma_\pi + \gamma_{\mathrm{p}})$] and to either the loss of one brood or to a constant investment in each brood [i.e., $a^* = 0, 1, a(0)$] depending on how related the mother is to the broods (i.e., depending on whether $r_{1\mathrm{m}} < r_{2\mathrm{m}} s_{\mathrm{m}}$, $r_{1\mathrm{m}} > r_{2\mathrm{m}} s_{\mathrm{m}}$, or $r_{1\mathrm{m}} = r_{2\mathrm{m}} s_{\mathrm{m}}$, respectively). I assume that maternal survival is such that the mother is favored to produce two broods in the absence of helping; so I let $s_{\mathrm{m}} = r_{1\mathrm{m}} / r_{2\mathrm{m}}$. For diploids, this means that $s_{\mathrm{m}} = 1$ while for haplodiploids s_{m} can be smaller than one. A survival $s_{\mathrm{m}} = 1$ can refer to the case in which the mother produces and provisions the offspring of both broods at once (mass provisioning), while second-brood offspring hatch from their eggs later. The assumption of $s_{\mathrm{m}} = r_{1\mathrm{m}} / r_{2\mathrm{m}}$ can be relaxed in more complex models incorporating selection pressures for producing two broods.

Offspring control

I consider a modified model where first-brood subjects stay spontaneously (i.e., without maternal influence) in the natal nest for some period of their adulthood. Subjects are here understood as a subset of first-brood offspring in which the staying propensity is expressed

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(e.g., females only or both sexes). A first-brood subject stays spontaneously with probability x_1. The survival of a first-brood subject offspring is now

$$s_1 = \sigma_1 \{\zeta_1 [x_1(s_0 - c) + (1 - x_1)s_0] + (1 - \zeta_1) \times 0\} \tag{A12a}$$

$$= \sigma_1 \zeta_1 (s_0 - c x_1). \tag{A12b}$$

The average probability of staying spontaneously among the first-brood subjects of a mother is X. The survival of a second-brood offspring is now

$$s_2 = \sigma_2 \left\{\zeta_2 \left[X s_{2\mathrm{p}} + (1 - X) s_0\right]\right. \tag{A13a}$$

$$\left. + (1 - \zeta_2) [X s_{2\mathrm{n}} + (1 - X) \times 0]\right\} \tag{A13b}$$

$$= \sigma_2 \left\{s_0 \zeta_2 + X \left[\zeta_2 (s_{2\mathrm{p}} - s_0) + (1 - \zeta_2) s_{2\mathrm{n}}\right]\right\}, \tag{A13c}$$

with the exact and approximated s_{2k} defined as before.

I also solve system (A9) numerically for this model using the approximations of s_{2k} in eqs. (A7). However, for a sufficiently small ratio of helpers to recipients $[n_{\mathrm{p}1}/n_2 \leq (s_{\max} - s_0)/b_{\mathrm{p}}, s_{\max}/b_{\mathrm{n}}]$, using the exact s_{2k} and letting x denote the population average staying probability, the dynamic equations are

$$\frac{dx}{dt} = \frac{1}{2} V_x n_{\mathrm{p}1} (b r_{21} s_{\mathrm{m}} - c r_{11}) \tag{A14a}$$

$$\frac{da}{dt} = \frac{1}{2} V_a \frac{R}{\gamma_{\mathrm{p}}} \{s_0 [(1 - e_1) r_{1\mathrm{m}} - (1 - e_2) r_{2\mathrm{m}} s_{\mathrm{m}}] + x(1 - e_1)(b r_{2\mathrm{m}} s_{\mathrm{m}} - c r_{1\mathrm{m}})\} \tag{A14b}$$

$$\frac{de_1}{dt} = -\frac{1}{2} V_{e_1} a \frac{R}{\gamma_{\mathrm{p}}} [s_0 r_{1\mathrm{m}} + x (b r_{2\mathrm{m}} s_{\mathrm{m}} - c r_{1\mathrm{m}})] \tag{A14c}$$

$$\frac{de_2}{dt} = -\frac{1}{2} V_{e_2} (1 - a) \frac{R}{\gamma_{\mathrm{p}}} \left\{s_0 r_{2\mathrm{m}} s_{\mathrm{m}} - x \frac{n_{\mathrm{p}1}}{n_2} \frac{1}{e_2} \left[(b_{\mathrm{n}} - b_{\mathrm{p}}) r_{2\mathrm{m}} s_{\mathrm{m}} - (c_{\mathrm{n}} - c_{\mathrm{p}}) r_{1\mathrm{m}}\right]\right\}. \tag{A14d}$$

Demographic variables

The ecologically asymptotic population growth rate is λ, which is given by the only real solution of the characteristic equation of $\mathbf{W}$; that is, by $\lambda^3 = \lambda f_1 s_1 + s_{\mathrm{m}} f_2 s_2$. Setting $\lambda = 1$,

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the ecological equilibrium frequencies of class-i individuals are

$$u_{\mathrm{m}} = \frac{1}{1 + f_1 + s_{\mathrm{m}}(1 + f_2)} \tag{A15a}$$

$$u_{\mathrm{M}} = u_{\mathrm{m}} s_{\mathrm{m}} \tag{A15b}$$

$$u_1 = u_{\mathrm{m}} f_1 \tag{A15c}$$

$$u_2 = u_{\mathrm{m}} s_{\mathrm{m}} f_2, \tag{A15d}$$

and the reproductive values of class-i individuals are

$$v_{\mathrm{m}} = \frac{1}{u_{\mathrm{m}} \Lambda} \tag{A16a}$$

$$v_{\mathrm{M}} = v_{\mathrm{m}} f_2 s_2 \tag{A16b}$$

$$v_1 = v_{\mathrm{m}} s_1 \tag{A16c}$$

$$v_2 = v_{\mathrm{m}} s_2, \tag{A16d}$$

all evaluated at population-average values.

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1 Parameter values

To calculate regression relatednesses, I use the following expressions:

$$\rho_{i\mathrm{m}} = \sigma_i \rho_{\mathrm{dm}} + (1-\sigma_i)\rho_{\mathrm{sm}} \tag{S1a}$$

$$\rho_{21} = \sigma_1\sigma_2\rho_{\mathrm{S}♀} + \sigma_1(1-\sigma_2)\rho_{\mathrm{b}♀} + (1-\sigma_1)\sigma_2\rho_{\mathrm{S}♂} + (1-\sigma_1)(1-\sigma_2)\rho_{\mathrm{b}♂}, \tag{S1b}$$

where the subscripts d, s, S, and b refer to daughter, son, sister, and brother respectively. Eqs. (S1) are in terms of standard regression relatedness values that can be obtained from pedigrees given the model assumptions (Hamilton, 1972).

I make the following assumptions. The mother is singly mated. For diploids, both broods have an even sex ratio. For haplodiploids, the second brood has an even sex ratio while the mother directs her influence only to first-brood females (so $\sigma_1 = 1$). Survival of young mothers to old mothers is such that mothers are initially favored to produce two broods (so $s_{\mathrm{m}} = r_{1\mathrm{m}}/r_{2\mathrm{m}}$). However, this value was obtained for the exact survivals, so it is an approximation when using the approximated survival in eqs. (A7) in the main text. Therefore, I let maternal resource allocation evolve alone for 1000 generations to properly initialize the numerical solutions. I let all traits have the same genetic variance to avoid giving an evolutionary advantage to any of them. I let the cost of acquiescence when raising maternally neglected offspring equal the baseline survival ($c_{\mathrm{n}} = s_0$), which amounts to saying that helpers of maternally neglected offspring are sterile. I take the initial probability of maternal influence and resistance to be small. I let the initial maternal allocation to be such that the mother produces two equally large broods that she feeds entirely. For simplicity, I let the energetic cost of producing and feeding offspring be the equal. I take the environmental resource to be such that population size is in the tens of thousands.

Finally, I assume that maternally neglected offspring use help more efficiently than maternally provisioned offspring ($b_{\mathrm{n}} > b_{\mathrm{p}}$). To reduce the parameter space, I consider two cases: strong and weak advantage in help use efficiency. Specifically, I take b_{n} to be as illustrated in Supporting Fig. 1. So, the benefit to maternally neglected offspring is $b_{\mathrm{n}} = b_{\mathrm{p}} d s_{\max}/(d s_{\max} - s_0)$, where $d = 1, 2$ for strong and weak advantage in help use efficiency respectively.

The remaining parameters are s_0, $s_{\max}$, c_{p}, and b_{p}. From their definitions, they can take values while satisfying $0 < s_0 < s_{\max} \leq 1$, $c_{\mathrm{p}} \leq s_0$, and $b_{\mathrm{p}} > 0$. With these assumptions, parameter values are those in Supporting Table 1 except when noted otherwise.

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Supporting Table 1: For Fig. 3 and Supporting Figs. 9-14, $t_{\text{final}} = 50\,000$ while $b_{\text{p}} \in [0,1]$ and $c_{\text{p}} \in [0, s_0]$. To properly initialize the numerical solutions, genetic variances are $\hat{V}_p = \hat{V}_q = \hat{V}_x = 0$, $\hat{V}_{e_i} = V_{e_i} \times 1000$, and $\hat{V}_a = V_a \times 1000$ for $t < 1000$. *The variance of e_i is scaled so that the additive effect of genes for traits e_i is equal to those for the other traits. †Values taken from Bulmer (1994) following Hamilton (1972).

E	100 000	For diploids			
V_p, V_q, V_a	0.01	σ_1, σ_2		0.5	
$V_{e_1}, V^*_{e_2}$	$0.01\left(1 - \frac{\gamma_\pi}{\gamma_\pi + \gamma_{\text{p}}}\right) = 0.005$	η_1, η_2		0.5	
$\gamma_\pi, \gamma_{\text{p}}$	1	$\rho_{1\text{m}}, \rho_{2\text{m}}$		0.5†	
s_0	0.1	ρ_{21}		0.5†	
s_{max}	0.21	s_{m}		$\frac{r_{1\text{m}}}{r_{2\text{m}}} = 1$	
c_{p}	$s_0 = 0.1$	b_{p}		0.253	
c_{n}	$s_0 = 0.1$	b_{n}		$b_{\text{p}} \frac{s_{\text{max}}}{s_{\text{max}} - s_0} = 0.483$	
$p(0), q(0)$	0.01	For haplodiploids			
$e_1(0), e_2(0)$	$\frac{\gamma_\pi}{\gamma_\pi + \gamma_{\text{p}}} = 0.5$	σ_1	1	σ_2	0.5
$a(0)$	0.5	$\eta_{♀}$	0.5	$\eta_{♂}$	1
$t_{\text{final}} =$	15 000	η_1	0.5	η_2	0.75
		ρ_{dm}	0.5†	ρ_{sm}	1†
		$\rho_{\text{S}♀}$	0.75†	$\rho_{\text{b}♀}$	0.5†
		$\rho_{\text{S}♂}$	0.25†	$\rho_{\text{b}♂}$	0.5†
		$\rho_{1\text{m}}$	0.5	$\rho_{2\text{m}}$	0.75
		ρ_{21}		0.625	
		s_{m}		$\frac{r_{1\text{m}}}{r_{2\text{m}}} \approx 0.8889$	
		b_{p}		0.291	
		b_{n}		$b_{\text{p}} \frac{s_{\text{max}}}{s_{\text{max}} - s_0} = 0.555$	

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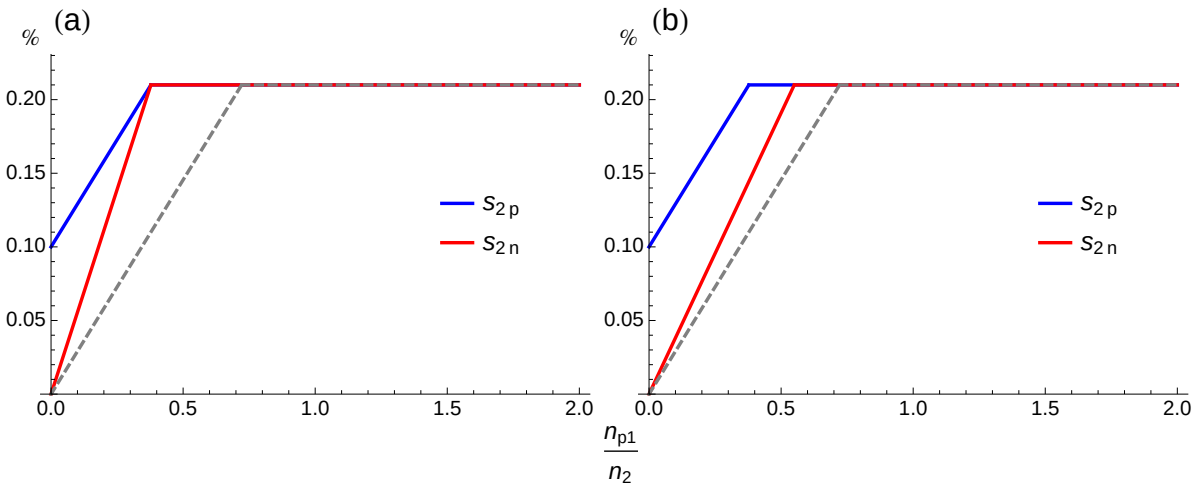
2 Supporting figures



Supporting Figure 1: Survival of recipients of help. Plots are the survival of helped second-brood offspring that are maternally provisioned (blue lines) or maternally neglected (red lines) vs. the number of helpers over recipients. The slope of the red line is the survival benefit from being helped for maternally neglected offspring [which for small n_{p1}/n_2 is $b_n = b_p d s_{max}/(d s_{max} - s_0)$]. The advantage in help use efficiency by maternally neglected offspring is either (a) strong ($d = 1$) or (b) weak ($d = 2$). The dashed gray line is the survival of helped maternally neglected second-brood offspring when they have no advantage in help use efficiency ($b_n = b_p$). Parameter values are those for haplodiploids in the Supporting Table. 1.

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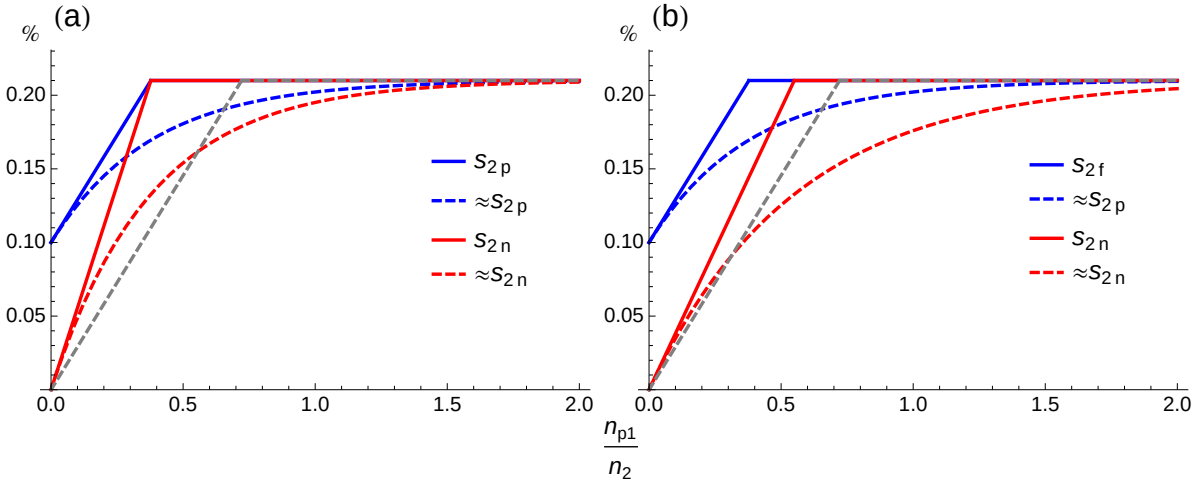

Supporting Figure 2: Approximations of recipients' survival. See legend of Supporting Fig. 1. Dashed lines are the approximated survival of helped second-brood offspring that are maternally provisioned (blue) or maternally neglected (red). Such approximations were used to obtain all numerical solutions.

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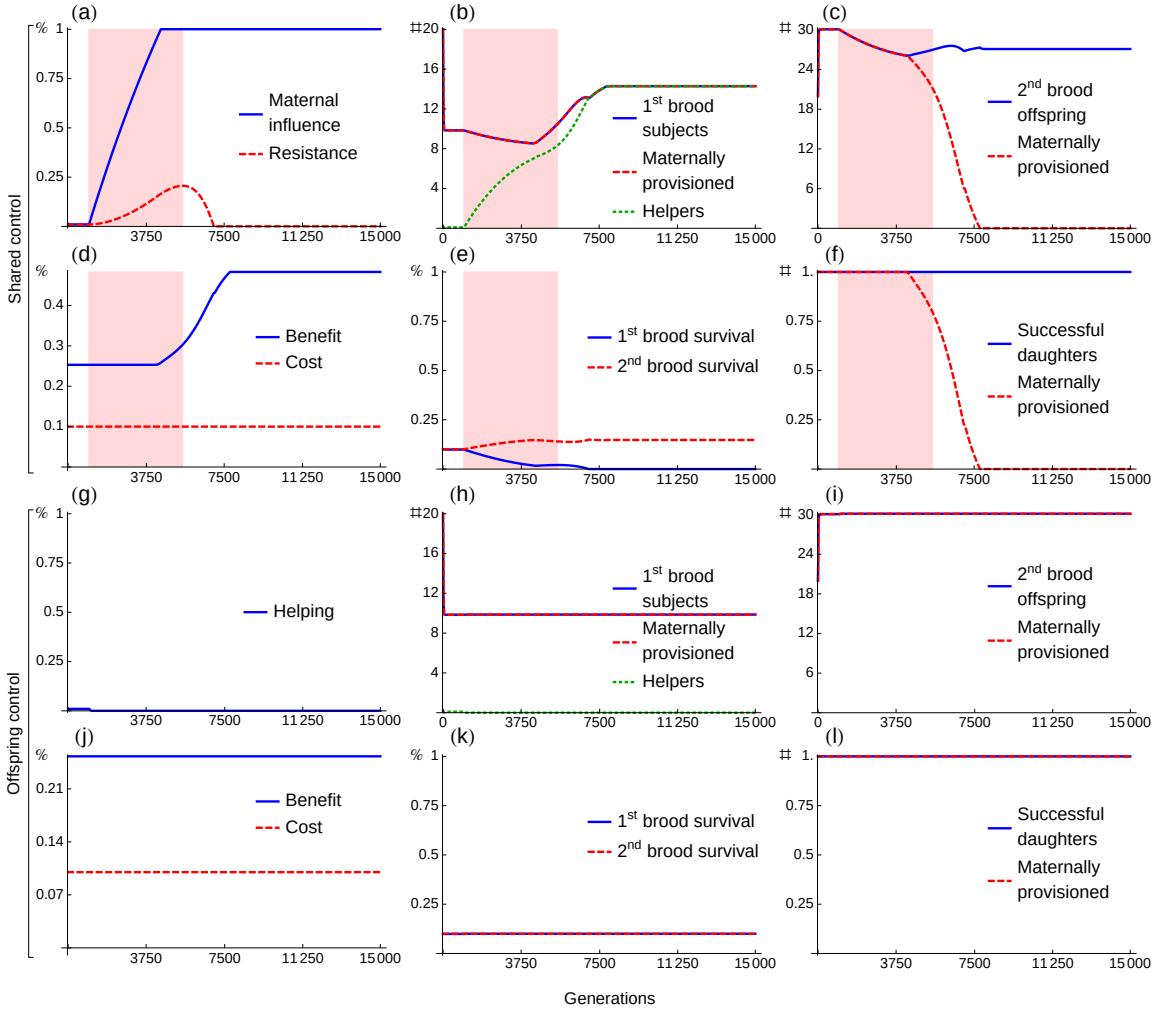

Supporting Figure 3: Stable eusociality via maternal manipulation with costless resistance in diploids. See legend of Fig. 2. Parameter values are in the Supporting Table 1.

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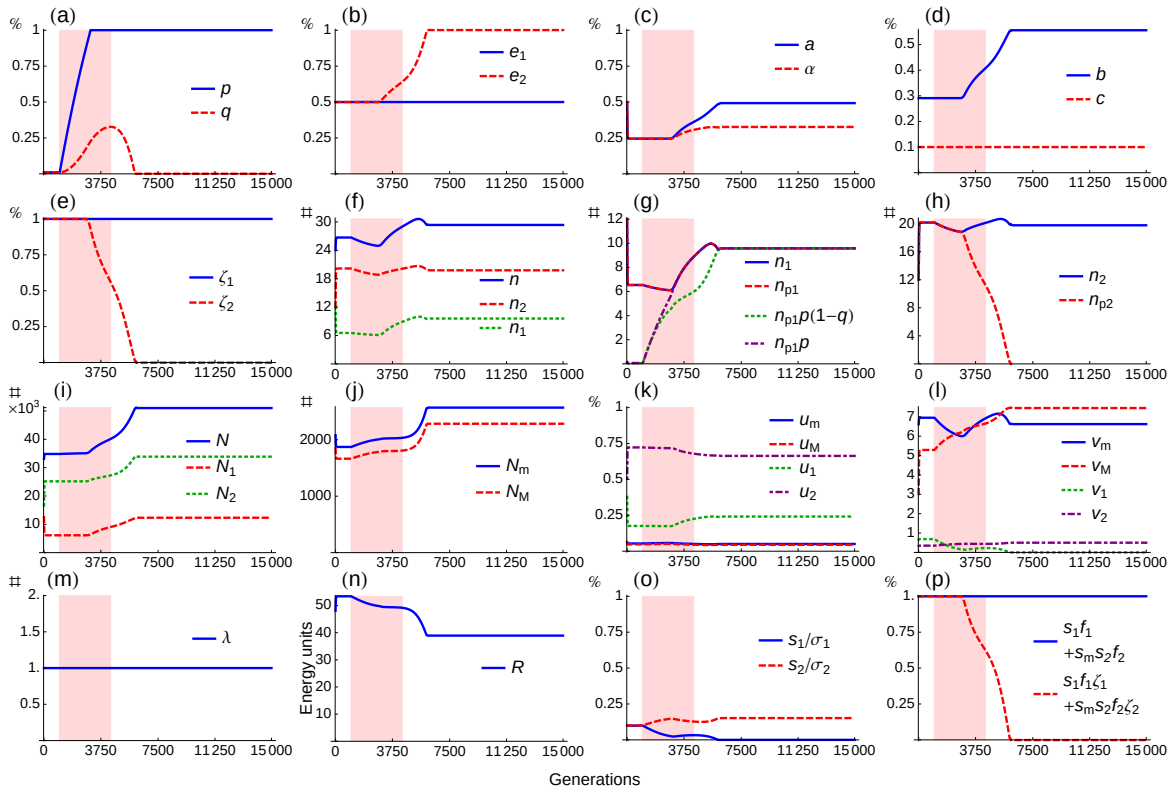

Supporting Figure 4: Detailed dynamics for haplodiploids under shared control. See legend of Fig. 2a-f. See Table 2 for definitions of variables. (b) The mother increases her investment in producing second-brood offspring. (h) The number of second-brood offspring remains largely constant. (i) Population size start to increase in evolutionary time when the mother increases here investment in second-brood offspring production. (m) Population size remains constant in ecological time since the ecologically asymptotic population growth rate remains 1. (n) Maternal resource decreases when the average offspring survival increases. (l) Reproductive values evolve and old mothers and second-brood offspring become more valuable. (g) $n_{\mathrm{p1}}p(1-q)$ is the number of helpers. (o) s_i/σ_i is the probability that a brood-i offspring becomes a parent. (p) $s_1 f_1 + s_{\mathrm{m}} s_2 f_2$ is the number of daughters that become mothers weighted by maternal genetic contribution. $s_1 f_1 \zeta_1 + s_{\mathrm{m}} s_2 f_2 \zeta_2$ is the number of them that are maternally provisioned.

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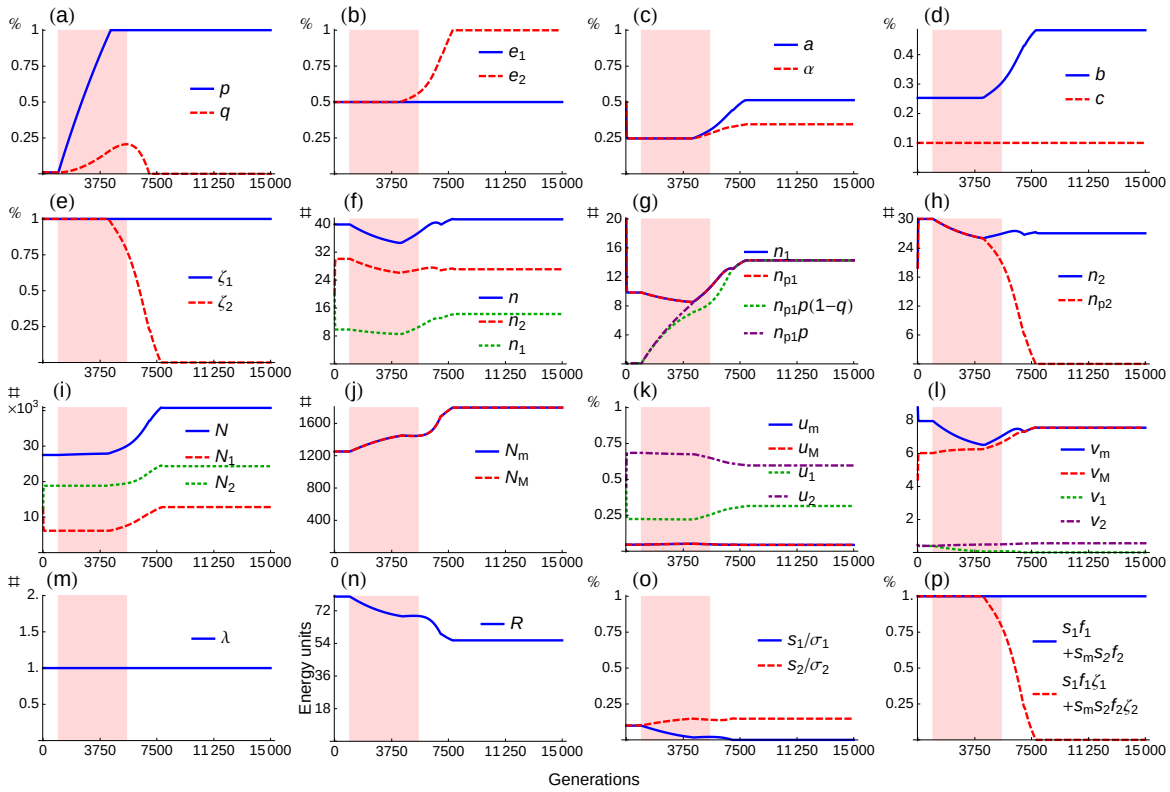

Supporting Figure 5: Detailed dynamics for diploids under shared control. See legend of Supporting Figs. 3a-f and 4.

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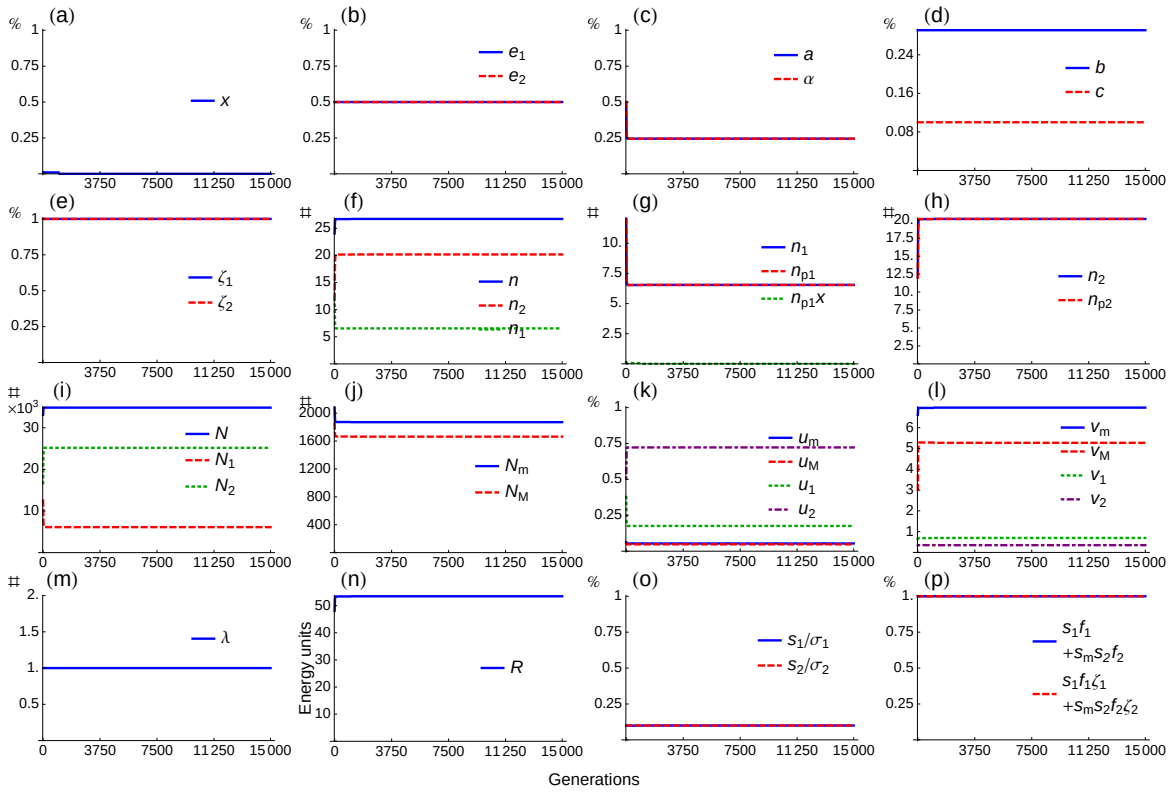

Supporting Figure 6: Detailed dynamics for haplodiploids under offspring control. See legend of Fig. 2g-l and Supporting Fig. 4. (a) x is the population-average probability that a first-brood subject stays in the natal nest in the absence of maternal influence.

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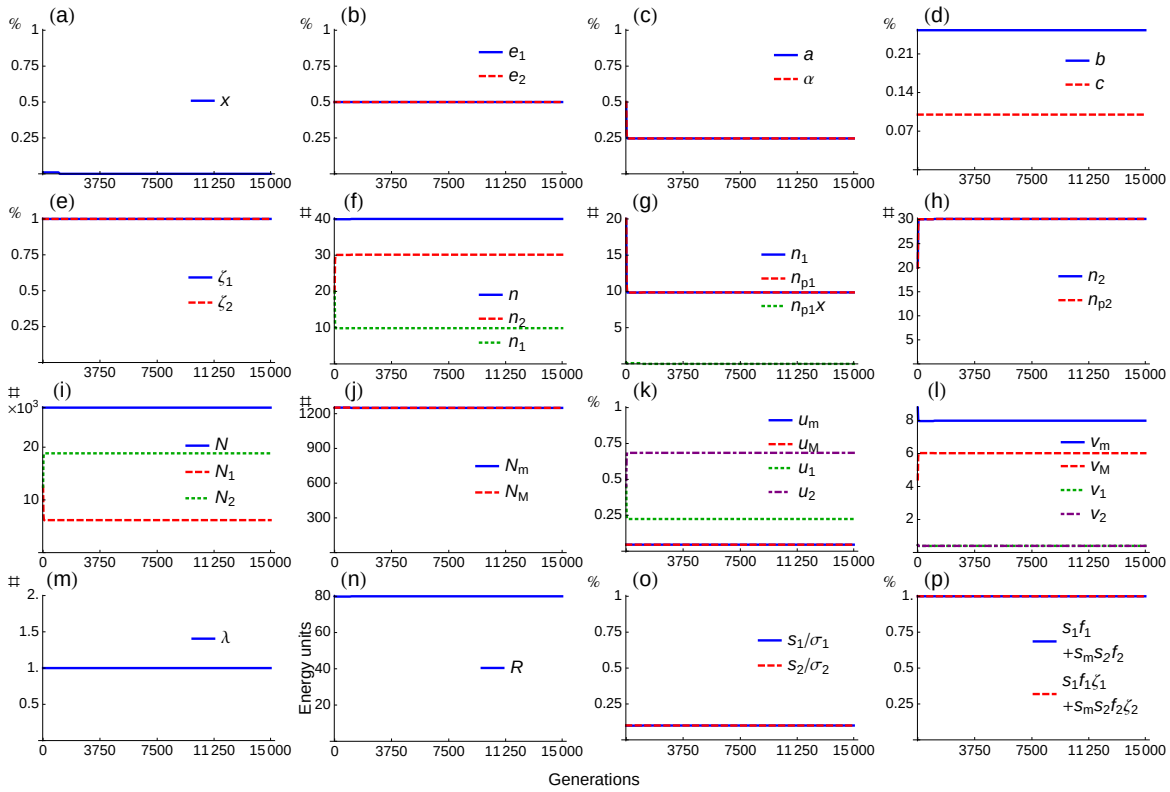

Supporting Figure 7: Detailed dynamics for diploids under offspring control. See legend of Supporting Figs. 3g-l and 6.

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Supporting Figure 9-14: Parameter space exploration. See legend of Fig. 3 in the main text. Baseline survival is small ($s_0 = 0.1$) in Supporting Figs. 9 and 10; intermediate ($s_0 = 0.3$) in Supporting Figs. 11 and 12, and large ($s_0 = 0.5$) in Supporting Figs. 13 and 14. The advantage of maternally neglected offspring in help use efficiency is strong ($d = 1$) for Supporting Figs. 9, 11, and 13; and weak ($d = 2$) for Supporting Figs. 10, 12, and 14. For certain regions, one of the broods is absent in the end ($n_i < 1$) as the mother devotes most of her resources toward one of them (Supporting Figs. 10b, 11b, 12a,b, 13b, and 14a,b; bordering lines with no eusociality are not shown). The remaining parameter values are in Supporting Table 1.

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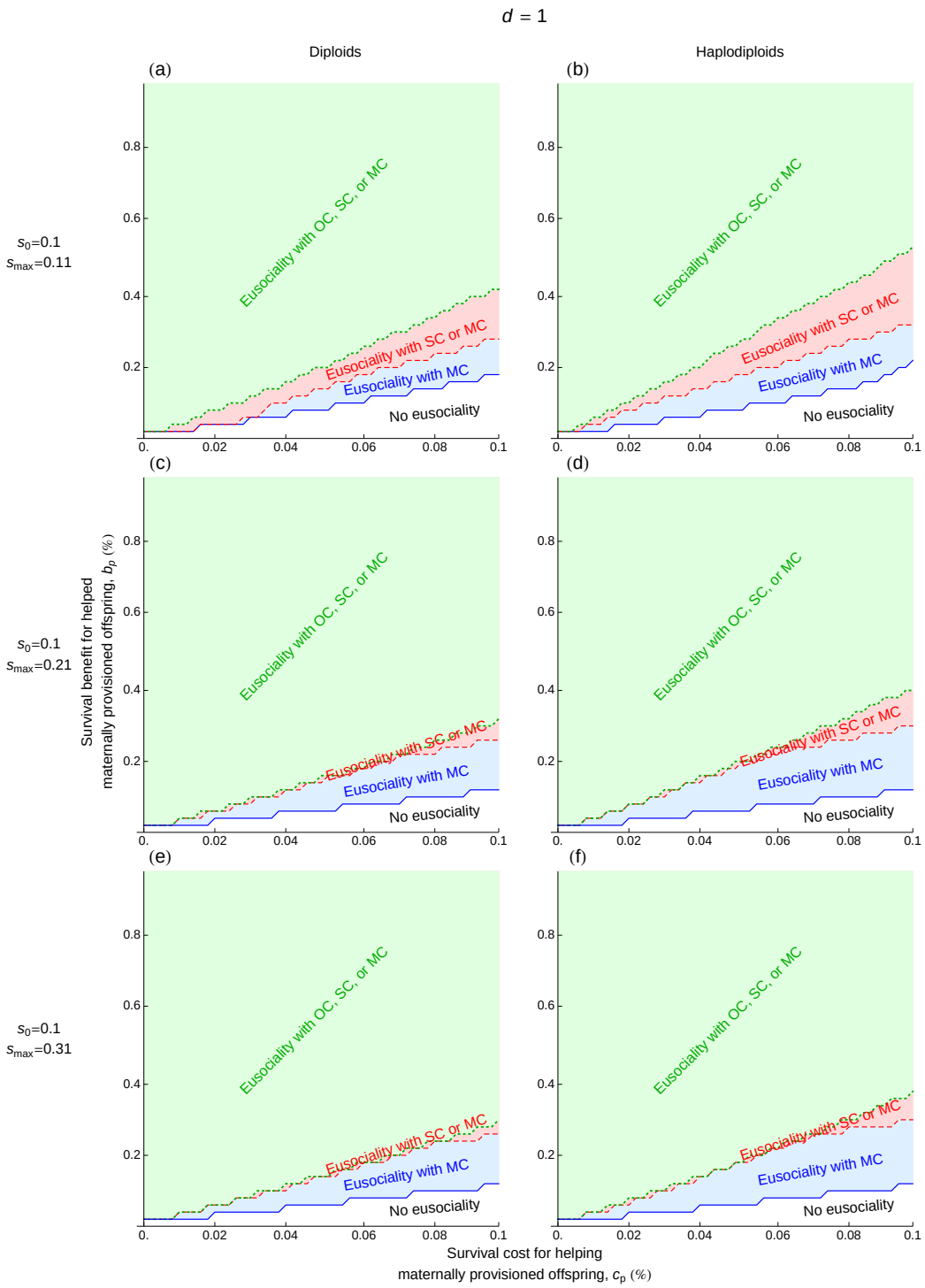

Supporting Figure 9

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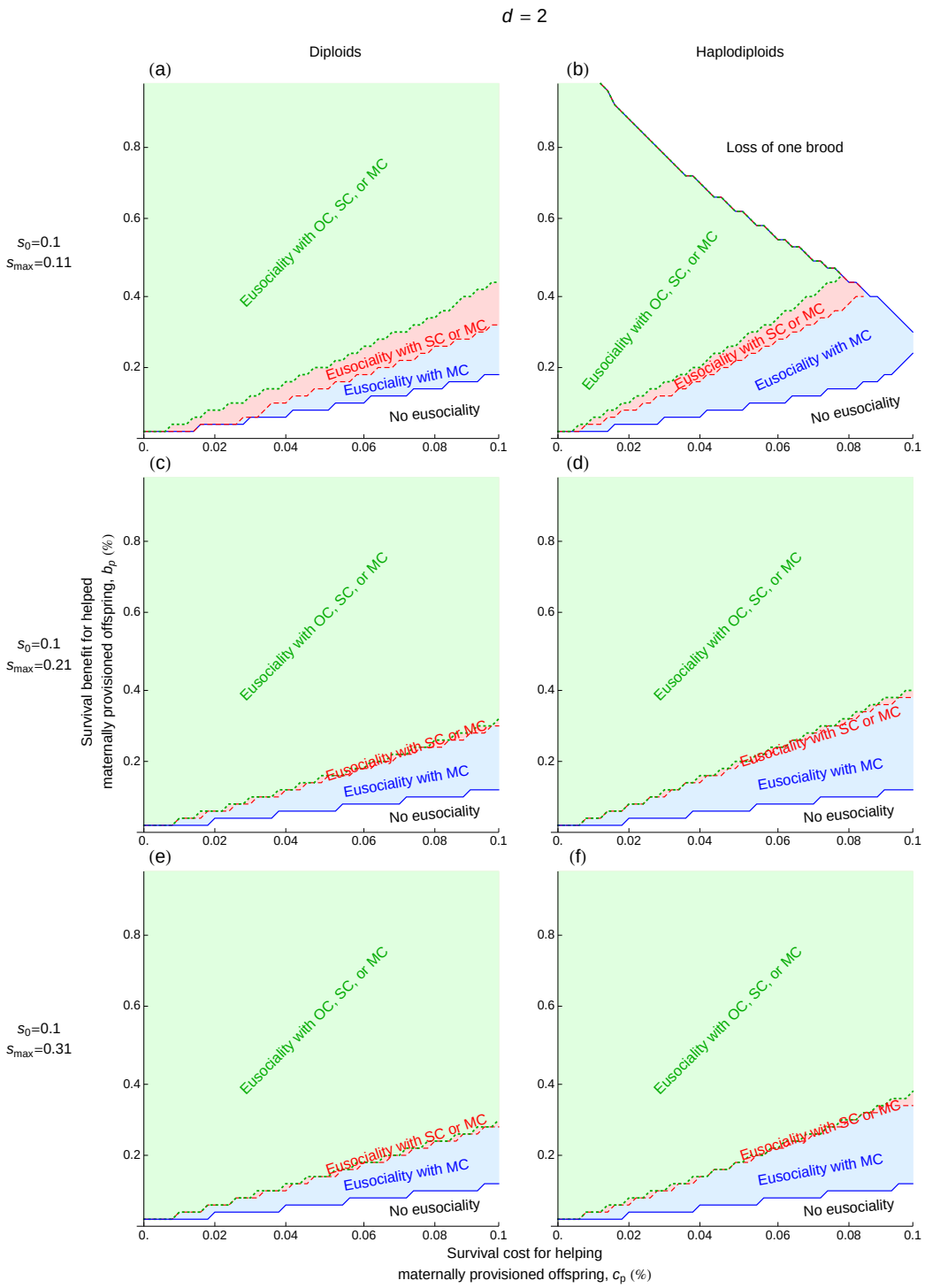

Supporting Figure 10

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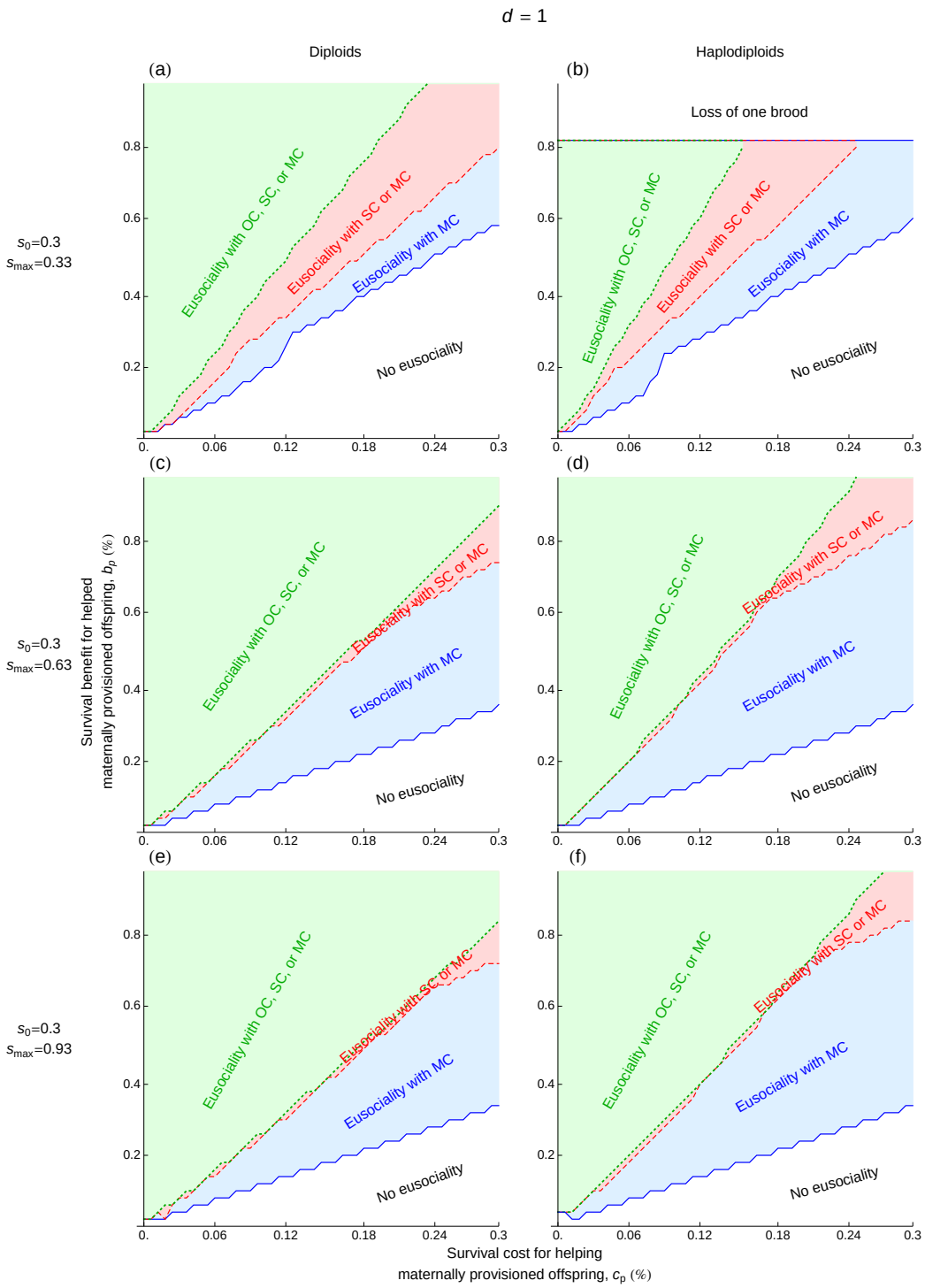

Supporting Figure 11

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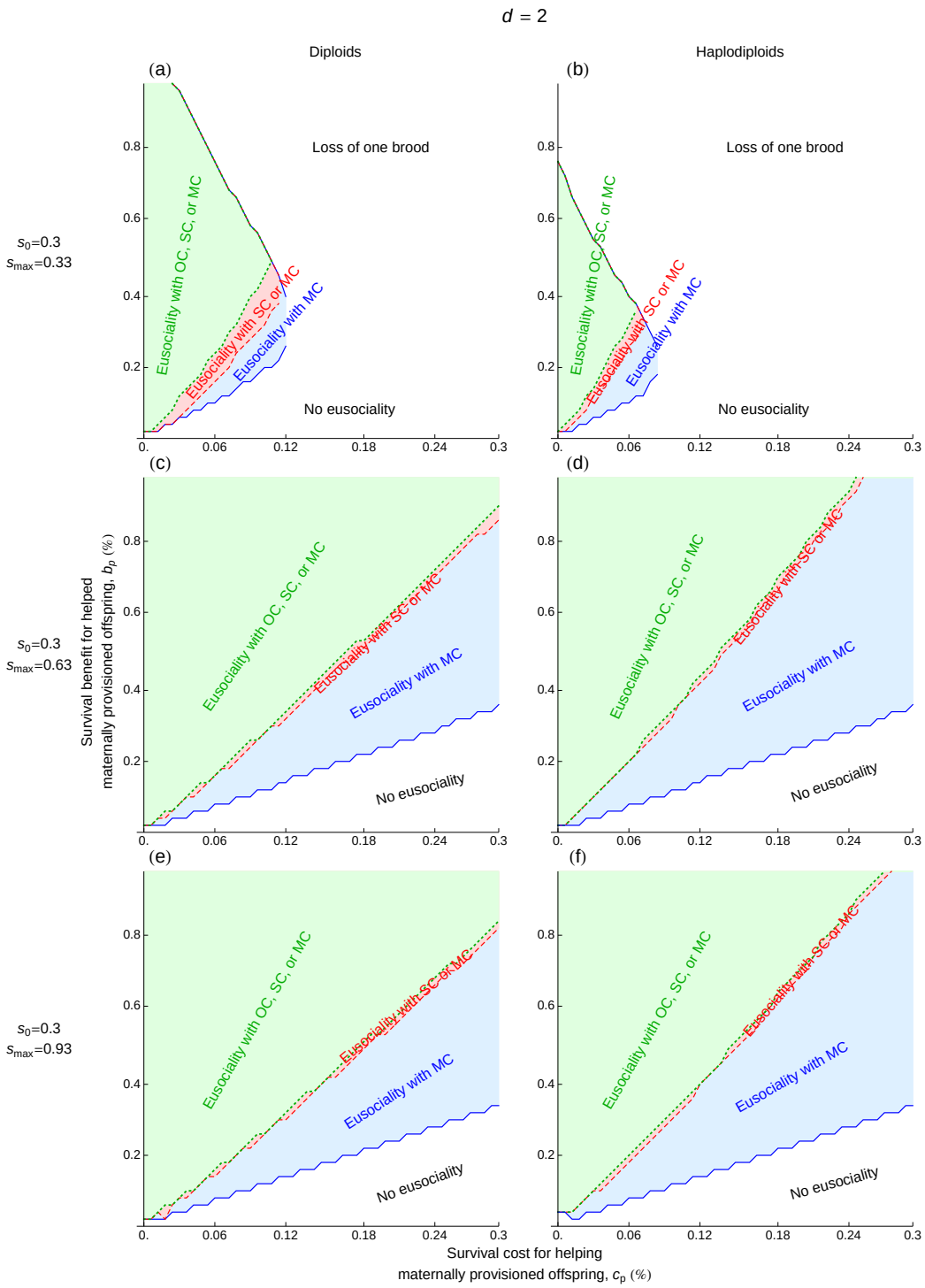

Supporting Figure 12

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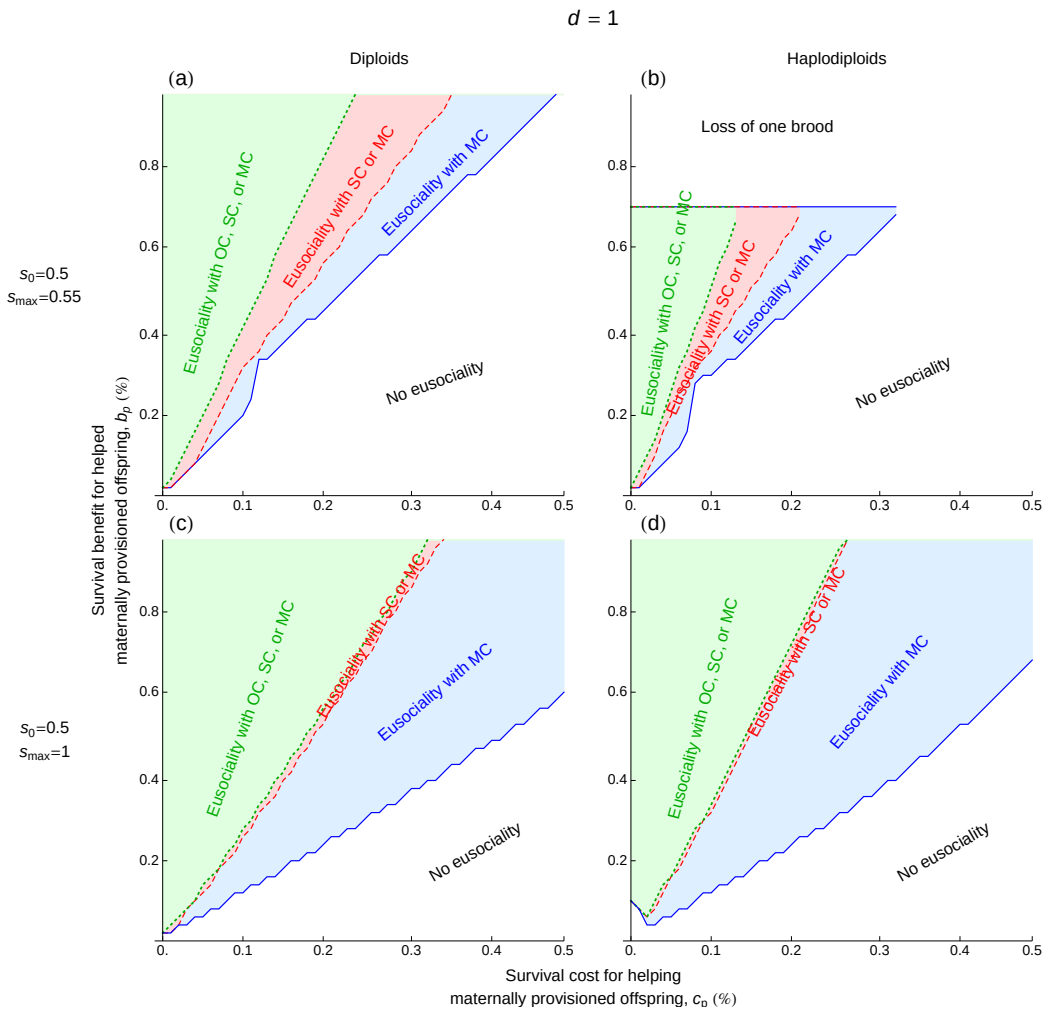

Supporting Figure 13

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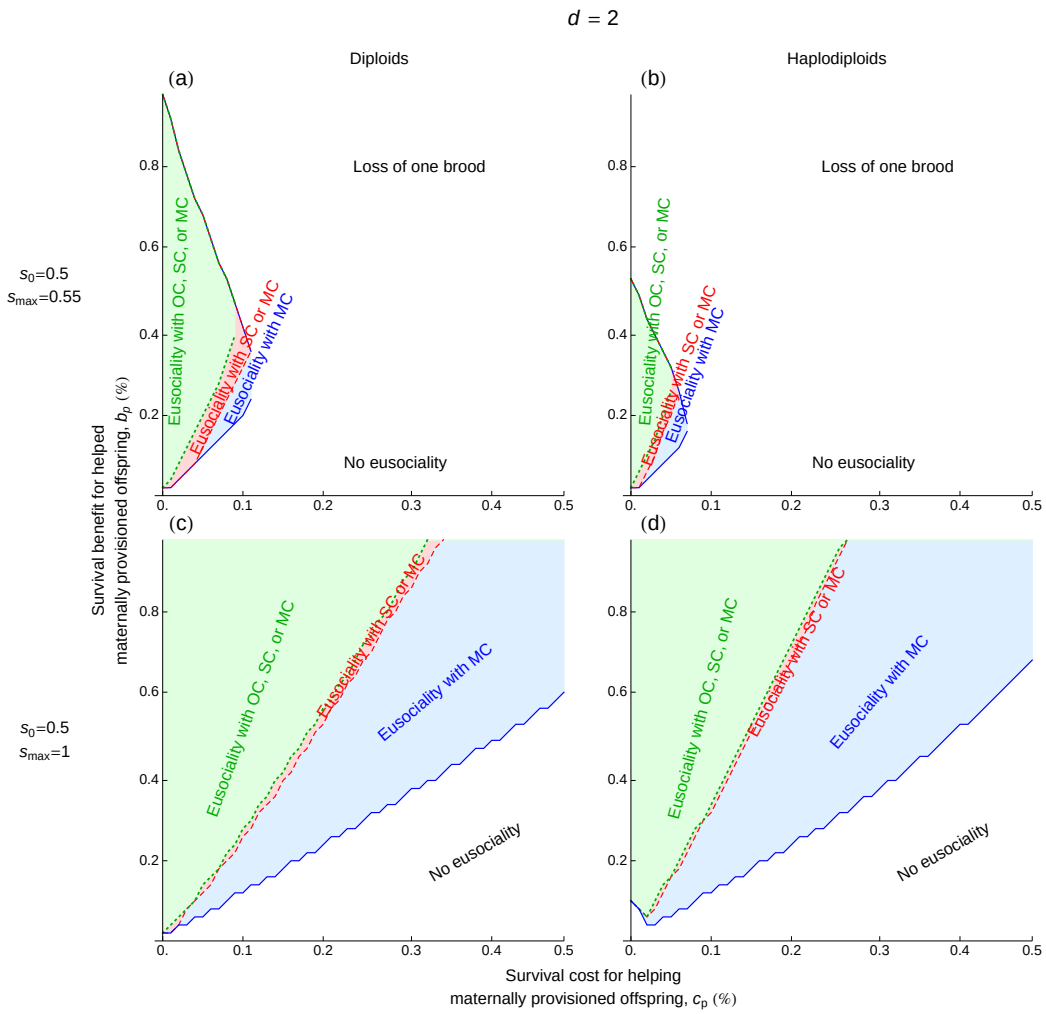

Supporting Figure 14

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