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Evolutionary biology

Resolving the evolution of sterile worker castes: a window on the advantages and disadvantages of monogamy

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Many social Hymenoptera species have morphologically sterile worker castes. It is proposed that the evolutionary routes to this obligate sterility must pass through a 'monogamy window', because inclusive fitness favours individuals retaining their reproductive totipotency unless they can rear full siblings. Simulated evolution of sterility, however, finds that 'point of view' is critically important. Monogamy is facilitating if sterility is expressed altruistically (i.e. workers defer reproduction to queens), but if sterility results from manipulation by mothers or siblings, monogamy may have no effect or lessen the likelihood of sterility. Overall, the model and data from facultatively eusocial bees suggest that eusociality and sterility are more likely to originate through manipulation than by altruism, casting doubt on a mandatory role for monogamy. Simple kin selection paradigms, such as Hamilton's rule, can also fail to account for significant evolutionary dynamics created by factors, such as population structure, group-level effects or non-random mating patterns. The easy remedy is to always validate apparently insightful predictions from Hamiltonian equations with life-history appropriate genetic models.

1. Introduction

The key character of eusociality is reproductive division of labour within collaborative groups. One or a limited number of individuals (queens) produce most or all of the offspring, while 'workers' forego reproduction for group beneficial activities. Colonies in eusocial species are primarily composed of relatives, although whether high genetic relatedness is essential to evolving reproductive castes or merely a by-product of group formation is hotly debated [1–4]. If close kinship does matter, then monogamy would be a facilitating pre-adaptation for subsequent eusocial evolution by creating cohorts of full siblings. Support for this monogamy hypothesis comes from several phylogenetic analyses, that find cooperative breeding or eusociality in mammals, birds and Hymenoptera probably evolved from solitary ancestors that were either monogamous or with reduced promiscuity [5–7].

The monogamy hypothesis for eusociality is less consistently supported theoretically when the evolution of 'helping' is compared across full and half-sib offspring cohorts. Differing models produce a variety of outcomes: (i) polygamy is generally more facilitating for spreading eusociality in populations [8]; (ii) both monogamy and haplodiploidy facilitate eusociality more than polygamy and diploidy [9] and (iii) relative advantage from monogamy or polygamy depends on the degree of local resource competition between siblings [10]. Boomsma [11] points out that these models consider facultative helping in totipotent offspring rather than testing the original monogamy hypothesis for evolution of obligately sterile social insect castes. Hence, the model here assumes a species that has evolved to a level of stable eusociality where reproductive success requires the presence of both a queen and offspring workers. In such species, virgin queens can never initiate or successfully head a colony because they cannot produce workers. Also

Table 1. Kin selection calculations for spread of sterility alleles based on Hamilton's rule. To maximize inclusive fitness, sterility is favoured when ratios of relatedness values for lost and gained relatives (r_l/r_g) are less than ratios of benefit to cost ($b/c = 1, 1.1$ or 2 with sterility benefits of $0, 10$ or 100%). Sterility occurs by either mothers being manipulative, workers being altruistic or subsociality where workers manipulate others into sterility. Expected rates of increase under monogamy (M) versus polygamy (P) are based on which strategy has the smaller r_l/r_g ratio. The observed outcomes are model simulations (figure 1).

| condition | loss (r_l) | gain (r_g) | r_l/r_g | outcomes |
|------------------|------------------------------------|--------------------------------|-----------|-------------------|
| manipulation (M) | grandkid = 0.25 | offspring = 0.50 | 0.50 | Exp. M = P |
| (P) | grandkid = 0.25 | offspring = 0.50 | 0.50 | Obs. M = P |
| altruism (M) | offspring = 0.50 | full sib ^a = 0.50 | 1.00 | Exp. M > P |
| (P) | offspring = 0.50 | mixed sibs ^b = 0.30 | 1.67 | Obs. M > P |
| subsocal (M) | nephew/niece = 0.375 | full sib ^a = 0.50 | 0.75 | Exp. P > M |
| (both sexes) (P) | mixed n's ^c = 0.175 | mixed sibs ^b = 0.30 | 0.58 | Obs. P > M; M > P |
| subsocal (M) | nephew = 0.375 | brother = 0.25 | 1.50 | Exp. P > M |
| (only sons) (P) | mixed nephews ^c = 0.175 | brother = 0.25 | 0.70 | Obs. P > M; M > P |

^aAverage of relatedness of sister and brother.

^bAverage when 20% are full sibs and 80% are half-sibs.

^cAverage when 20% are full sib offspring and 80% are half-sib offspring.

in such species workers cannot inherit nests because, although they retain some ability to reproduce, they are physiologically limited and cannot become highly fecund queens. Nonacs [8] focused on these two issues relative to the evolution of facultative helping and, therefore, they are not reconsidered here in order to test the monogamy hypothesis in its most straightforward formulation [11].

2. Material and methods

I simulate natural selection [3] acting on worker reproductive behaviour by tracking changes in frequency of 'obligate sterility' alleles in hypothetical haplodiploid Hymenopteran populations. Independent from the genetic model, kin-selective calculations of inclusive fitness can *a priori* predict whether allele frequencies should increase or decrease in the simulations. This, however, requires specifying where the alleles act. One possibility is that sterility alleles create manipulating mothers, where queens impose sterility on their offspring through diet, physical suppression or pheromonal signals [12,13]. A second possibility is through offspring altruism, where alleles cause workers to cede their reproduction to their mother. The final possibility is subsocial [14], where workers assume manipulating roles and enforce sterility on other siblings.

By Hamilton's rule, obligate sterility should be favoured [11] whenever benefit (b) provided to kin exceeds the cost (c) to self, or $r_g b > r_l c$ (r values = probability of being identical by descent for relatives gained (g) or lost (l)). Obligat sterility, therefore, is predicted when $b/c > r_l/r_g$ with the r value ratios depending on the point-of-view of who 'controls' sterility (table 1). That the controlling party can be either the mother, the worker themselves, or the cohort of non-reproductive siblings yields a separate Hamilton's rule for each. Calculating the r ratios for monogamy and polygamy shows that: (i) number of mates should have no effect on the predicted spread of sterility if based on manipulation by mothers; (ii) altruistic sterility by workers is more likely favoured through monogamy and (iii) sterility due subsocial actions is more favoured through polygamy.

The genetic simulations examined whether or not a trait for obligate sterility would spread to fixation in populations that varied in mate number and benefit for worker sterility (full details of the model are presented in the electronic supplementary material). In colonies, a given worker had one of two phenotypes:

(i) a worker that reproduced one offspring of their own or (ii) a worker that had ceded reproduction to its mother. Ceding reproduction could positively affect colony-level productivity, such as a large effect of two queen-produced offspring instead of the worker's single one. Thus, by Hamilton's rule the benefit of sterility here is twice its cost ($b = 2, c = 1$). A small effect creates a 10% increased queen productivity ($b/c = 1.1$). Finally, no additional benefit ($b/c = 1$) is also examined. A worker's phenotype depended on the genetic make-up of the colony. For maternal manipulation, obligate sterility was imposed on all workers as determined by the queen's genotype. For offspring altruism, a given worker's reproductive behaviour depended on whether or not it had a sterility-inducing genotype. For subsocial effects, a given worker's phenotype was a probabilistic function of the frequency of sterility alleles across the entire worker population.

3. Results

Hamilton's rule predicts that relatedness levels have no effect on selection for sterility (table 1) and that under b/c ratios considered, sterility is always favoured. These predictions are upheld (figure 1a). With worker altruism, sterility is predicted to be spread under monogamy when $b/c > 1$, but under polygamy only with $b/c = 2$. These predictions are also upheld (figure 1b). The same qualitative relationships are expressed with diploidy (electronic supplementary material). With subsocial effects, sterility spreads as predicted by Hamilton's rule with all three b/c values tested (figure 1c). If workers can produce males, obligate sterility also spreads as predicted by $b/c > r_g/r_l$ (figure 1d: the inequality is always met with polygamy, but only when $b/c = 2$ with monogamy). Contrary to predictions from Hamilton's rule about subsociality, however, obligate sterility increases faster with monogamy than with polygamy when $b/c > r_l/r_g$ and the benefit-to-cost ratio is large.

Viscosity and other population-level processes can lead to faulty predictions from the simplest form of Hamilton's rule [15] illustrated here through predicted subsocial outcomes being insensitive to group-level effects. Colonies with parents having sterility genotypes are more productive whenever $b > 1$. An example of how colony-level effects arise is apparent from examining the productivity of individual colonies in

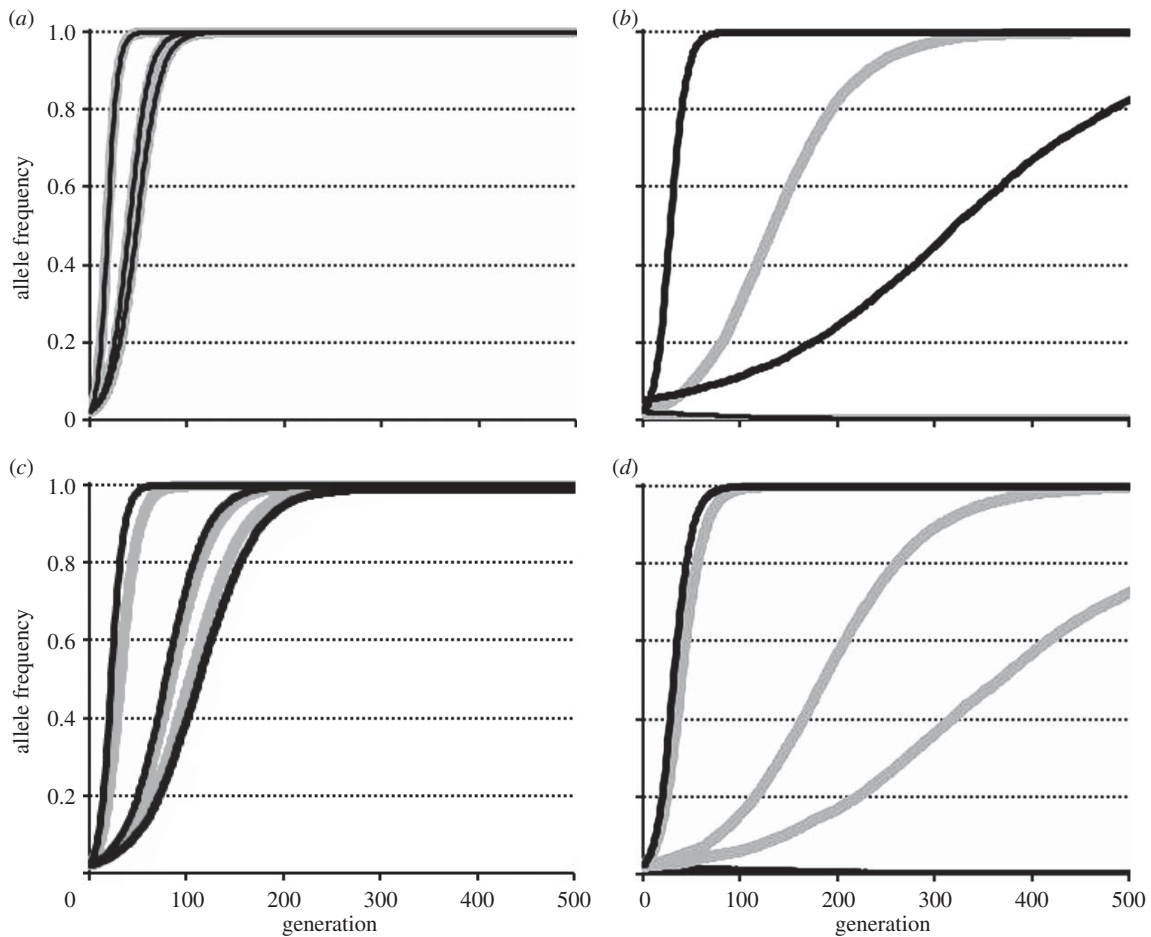


Figure 1. Changes in sterility allele mean frequencies. Monogamy and polygamy are represented by black and grey lines, respectively, with 100 replicates for each set of conditions. Benefit from sterility ranged from none (slowest rate of increase or fastest decrease in each panel's set), to 10 and 100% (fastest rate of increase in each set). Alleles produce sterility through (a) maternal manipulation, (b) altruism, or (c) sibsocial manipulation suppressing either production of both sexes, or (d) only males. Note that in (b) and (d) sterility is lost from populations when $b/c < r/r_g$, as predicted by Hamilton's rule (table 1).

a sibsocial scenario when 50% of population alleles are for sterility (figure 2). The coefficient of variation in productivity across all colonies is greater with monogamy than with polygamy. Greater across-group variance with monogamy leads to stronger group-level selection. Therefore, sterility alleles that are favoured by kin selection can increase more rapidly with monogamy. This complementary effect of group-level selection appears in all figure 1 curves, where the fastest increases occur with intermediate frequencies of sterility alleles. Across-group variance is maximal at those frequencies and therefore, so is group-level selection.

4. Discussion

Theoretically, obligately sterile worker castes need not always evolve through a narrow monogamy window. Monogamy is the favourable preadaptation if: (i) sterility evolves as a self-sacrificial behaviour in workers or (ii) sterility through manipulation of developing offspring by siblings can significantly increase queen reproduction. Conversely, neither monogamy nor polygamy makes sterility more likely to be selectively favoured if effects arise through maternal manipulation. Finally, polygamy is the more favourable preadaptation if worker reproduction is already restricted to

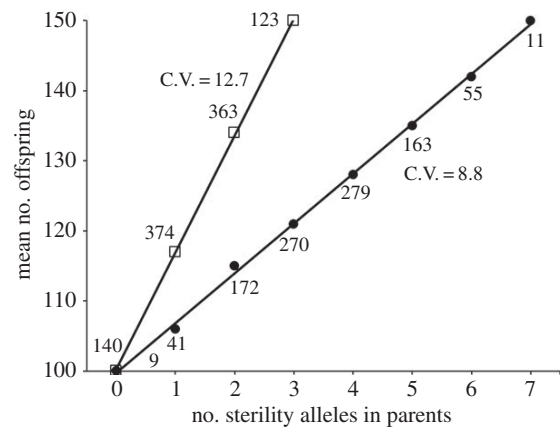


Figure 2. Offspring produced by colonies versus the number of sterility alleles in parents' genotypes. Sterility is a sibsocial effect and initially represents 50% of the population's alleles. The coefficient of variation in productivity is greater with monogamy (open squares) than with polygamy (dosed circles). Numbers refer to colonies in each category of allele distribution.

producing only sons and its suppression leads to little or no gain in queen-produced offspring.

The results clearly emphasize the importance of the genetic mechanisms that create phenotypes. Under identical

conditions of benefit, cost and mating biology, an allele for obligate sterility can spread if it affects maternal behaviour, but may not if it only affects worker behaviour. More broadly considered, if offspring sterility is favoured either as altruistic or sibsocial effects, it will be even more strongly favoured by mothers (i.e. compare slopes of curves in figure 1). This asymmetry in selective advantage suggests that the conceptual concentration on cooperation evolving through offspring maximizing their inclusive fitness may be misplaced or at least incomplete [1–4]. Instead, parental manipulation, effectively brought to bear on offspring, may more often drive the evolution of helping behaviour. Indeed, recent studies on facultative eusociality in the halictid bee, *Megalopta genalis*, strongly implicate mothers as being manipulative in causing daughters to become helpers [12,13]. Because the mothers control the amount and delivery of food, daughters may have no recourse but to acquiesce to manipulation.

In the models presented here, Hamiltonian inclusive fitness calculations accurately predict the general outcomes, such as when is obligate sterility selectively adaptive. Problems arise, however, if specific effects from genetic system dynamics, changing gene frequencies over time, population structure and group-level selection or non-random mating patterns are involved. A case in point is the disparate outcomes of two models on evolution of facultative helping behaviour. Nonacs [8] found that polygamy is often more facilitating for spreading cooperative behaviour and haplodiploidy versus diploidy has no effect. By contrast, Fromhage & Kokko [9] found that both monogamy and haplodiploidy are more facilitating for

cooperative evolution. Resolving these two outcomes is quite simple: Nonacs's model allows nest inheritance by daughters and Fromhage & Kokko's model does not. Nest inheritance creates an asymmetric genetic effect whereby only helpers with the cooperative genotype reap this advantage. Because polygamy creates more nests with helping daughters, the inheritance occurs more often and cooperation spreads more rapidly. If nest inheritance is added to [9], or prevented in [8], the predictions become identical (P. Nonacs 2013, unpublished results). The monogamy and haplodiploidy bias for the evolution of cooperation is not because of higher within-nest relatedness, but because of another asymmetric genetic pattern. Again because only certain genotypes can become helpers, in nests with both helper and non-helper daughters, the former is removed from the pool of future reproductives to the benefit of the latter. Both monogamy and haplodiploidy reduce the relative proportion of nests in a population experiencing this asymmetry in selection, thereby facilitating helping to spread [8].

Thus, one must be wary of simple kin-selective generalities such as monogamy and close genetic relatedness always increase the likelihood that cooperative behaviour or obligate sterility are selectively advantageous. One need to also examine under what range of conditions an explicit genetic model supports the statement. The phenomenon under consideration may be deceptively complex and affected by ecological and genetic details, not captured by one single Hamiltonian inequality.

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References

- Wilson DS, Wilson EO. 2007 Rethinking the theoretical foundation of sociobiology. *Q. Rev. Biol.* **82**, 327–348. (doi:10.1086/522809)
- Leigh EG. 2010 The group selection controversy. *J. Evol. Biol.* **23**, 6–19. (doi:10.1111/j.1420-9101.2009.01876.x)
- Nowak MA, Tarnita CE, Wilson EO. 2010 The evolution of eusociality. *Nature* **466**, 1057–1062. (doi:10.1038/nature09205)
- Bourke AFG. 2011 The validity and value of inclusive fitness theory. *Proc. R. Soc. B* **278**, 3313–3320. (doi:10.1098/rspb.2011.1465)
- Hughes WOH, Oldroyd BP, Beekman M, Ratnieks FLW. 2008 Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320**, 1213–1216. (doi:10.1126/science.1156108)
- Cornwallis CK, West SA, Davis KE, Griffin AS. 2010 Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969–972. (doi:10.1038/nature09335)
- Lukas D, Clutton-Brock T. 2012 Cooperative breeding and monogamy in mammalian societies. *Proc. R. Soc. B* **279**, 2151–2156. (doi:10.1098/rspb.2011.2468)
- Nonacs P. 2011 Monogamy and high relatedness do not preferentially favor the evolution of cooperation. *BMC Evol. Biol.* **11**, 58. (doi:10.1186/1471-2148-11-58)
- Fromhage L, Kokko H. 2011 Monogamy and haplodiploidy act in synergy to promote the evolution of eusociality. *Nat. Commun.* **2**, 397. (doi:10.1038/ncomms1410)
- Leggett HC, El Mouden C, Wild G, West S. 2012 Promiscuity and the evolution of cooperative breeding. *Proc. R. Soc. B* **279**, 1405–1411. (doi:10.1098/rspb.2011.1627)
- Boomsma JJ. 2013 Beyond promiscuity: mate-choice commitments in social breeding. *Phil. Trans. R. Soc. B* **368**, 20120050. (doi:10.1098/rstb.2012.0050)
- Kapheim KM, Bernal S, Smith A, Nonacs P, Wcislo W. 2011 Support for maternal manipulation of developmental nutrition in a facultatively eusocial bee, *Megalopta genalis* (Halictidae). *Behav. Ecol. Sociobiol.* **65**, 1179–1190. (doi:10.1007/s00265-010-1131-9)
- Kapheim KM, Smith AR, Ihle KE, Amdam GV, Nonacs P, Wcislo WT. 2012 Physiological variation as a mechanism for developmental caste-biasing in a facultatively eusocial sweat bee. *Proc. R. Soc. B* **279**, 1437–1446. (doi:10.1098/rspb.2011.1652)
- Linksvayer TA. 2006 Direct, maternal, and sibsocial genetic effects on individual and colony traits in an ant. *Evolution* **60**, 2552–2561. (doi:10.1111/j.0014-3820.2006.tb01889.x)
- Queller DC. 1992 Does population viscosity promote kin selection? *Trends Ecol. Evol.* **7**, 322–324. (doi:10.1016/0169-5347(92)90120-Z)