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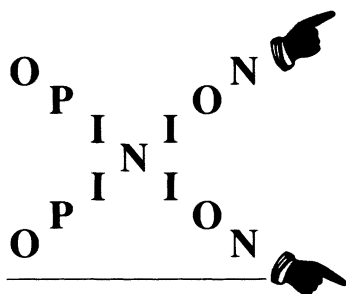
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Alloparental care and eusocial evolution: the limits of Queller's head-start advantage

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Summary. Queller (1989) proposes that the dependency of offspring on continued care by adults exerts great selective pressure for eusociality in polistine wasps. Daughters can reap large and immediate inclusive fitness benefits by becoming workers on their mother's nest via the 'head start' of having sibs already close to maturity. Queller concludes that this head-start advantage can exert selection intensity for eusociality that is up to 12 times as strong as the standard haplodiploid advantage. I argue, however, that the head-start hypothesis strongly predicts that one or two wasps should always remain on a given nest, but cannot explain why five or more wasps cooperate simultaneously. Therefore, instead of providing an evolutionary mechanism for true eusociality in Hymenoptera, the head-start hypothesis is more applicable to the broader phenomena of adoption or alloparental care in both diploid and haplodiploid species.

Polistine wasps need concerted care and feeding as larvae, and even as pupae require a parental presence or else they are sure to perish. Queller (1989) argues that this offspring dependence can serve as a powerful selective force that favors newly emerged wasps remaining on their natal nests to help their mother finish raising immature sibs, rather than initiating their own nests. His reasoning is that daughters get immediate inclusive fitness payoffs for worker-like behaviour because of their mother's "head start" in having already raised kin partway to maturity. As formulated, Queller's model proposes a mechanism for the evolution of worker behaviour that is up to 12 times stronger than standard models of haplodiploid advantages for raising sisters (Hamilton 1964). I argue here that, although the head-start hypothesis is mathematically sound, it has a much more limited effect on the evolution of eusociality than envisioned by Queller. The hypothesis fundamentally accounts for *serial* occupation of a nest by at least one wasp at a time, but not for *simultaneous* occupation of a nest by many wasps. It is the latter phenomenon which

any theory of eusocial evolution must explain. I will further suggest that an overlooked, novel insight of Queller's head-start hypothesis pertains to the broader question of the adoption of immature conspecifics or alloparental care in both diploid and haplodiploid species.

The head-start model

The head-start hypothesis requires that either the mother begins with more larvae than she can expect to raise alone under average circumstances, or that the mother is likely to die before her offspring reach maturity, which will doom them if left unattended (Queller 1989: 3225–3226). For a daughter to favor staying on her natal nest requires that:

$$rsb < r^*s^*b^*, \quad (1)$$

where the left-hand side of the equation is the fitness for starting her own nest: with r being the relatedness of her own offspring ($=0.5$), s the probability of her surviving until offspring independence, and b the number of adults raised. The right-hand side is the fitness gain for staying on the natal nest. Queller begins with the assumption that $b^* = b$ so that daughters should adopt worker roles if:

$$r^* > s/2s^*. \quad (2)$$

From data on worker survivorship, Queller's best estimate of s is 0.057 for *Polistes exclamans*. Using his assumption that $s^* = 1$, this results in worker behaviour being favored as long as $r^* > 0.03$. In other words,

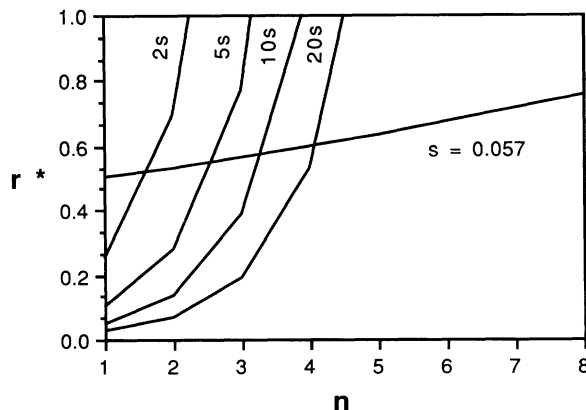


Fig. 1. The number of wasps (n) favored to remain on their natal nest as a function of the relatedness of the immature brood (r^*). n is plotted under two conditions: (1) where the mother has died and daughters' survivorship as solitary foundresses is equal to their survivorship on the natal nest ($s = [1 - d_w] = 0.057$), and (2) where all wasps have equal survivorship on the natal nest ($[1 - d] = 0.64$), which is from 2–20 times greater than solitary founding (s). Survivorship values are from Queller (1989) for *Polistes exclamans*.

voluntary assumption of worker roles by newly emerged females seems inevitable and almost independent of any haplodiploid advantages in relatedness.

I believe that Queller errs in setting $s^* = 1$ for remaining on the natal nest. This gives all daughters instantaneous fitness benefits for staying. That they never die or fail to help in increasing nest productivity could be true only if the brood were literally on the verge of independence. If this were the case, however, the presence of daughters would be unnecessary because b^* , the number of extra sibs raised due to the daughters' efforts, would become zero. Furthermore, this gives the 100th daughter that assumes a worker's role an identical fitness pay-off to that of the first worker.

It is more realistic to define s^* as the increase in colony survivorship due to a given daughter remaining with her natal nest. Consider the above-mentioned possibility of the original foundress dying. If one or more daughters remain as workers, then still dependent offspring have a chance to reach maturity. In fact, the probability that at least one adult is present until brood mature to independence is:

$$s_n = 1 - d_m \cdot (d_w)^n, \quad (3)$$

where d_m and d_w are the probabilities that either a mother (the original foundress) or a worker dies before the brood reaches independence, and n is the number of workers on the nest (all individuals are assumed to have an independent chance of dying). This formulation of the survival function is ecologically realistic, in that each additional worker adds proportionally less to overall nest survivorship and productivity (Michener 1964, Queller and Strassmann 1988, Strassmann et al. 1988).

Thus the effect of a daughter becoming the n th worker on a nest is:

$$s^* = s_n - s_{n-1}. \quad (4)$$

Gadagkar (1990) both first pointed out that setting $s^* = 1$ overestimates the fitness for working, and explicitly considered the consequences of b^* varying from 0 to b . He calculated a worker's fitness as the increase in nest productivity that directly results from her staying on the natal nest, prorated by her expected adult life span. In contrast to Queller's formulation, Gadagkar's model generates lower estimates of s^* and b^* for working (in his model these terms are redefined as σ^* and β^* , respectively). Consequently, head starts seem no longer as potent a force for favoring eusociality, ranging in five species, from 0.83–3.71 times the relative strength of Hamilton's (1964) haplodiploid advantage. However, Gadagkar concluded that this advantage was still a strong force favoring eusociality, because remaining on the natal nest gains "assured fitness returns" for any amount of work, while solitary founding pays off only if the foundress survives for the entire period of brood maturation. Although Gadagkar's model is more general than Queller's, it shares the same basic assumption: that any given amount of work results in an identical fitness payoff. Gadagkar's σ^* , like Queller's s^* , is a constant and not a dynamic function of the number of adults on the nest at the same time. Therefore, their models cannot be entirely accurate beyond the first wasp to join a nest.

To look at how the fitness of remaining at the natal nest is affected by the number of wasps already present, I used the data for *P. exclamans* with $s = 0.057$, $d_m = 0.36$ and $d_w = 0.943$ (Queller 1989). Therefore, the nest success rate with the original foundress as the only adult is $s_0 = 0.64$. If one daughter joins her, s_1 rises to only 0.66 and $s^* = 0.02$. Inserting this value into (2) requires that $r^* = 1.35$ for just one daughter to assume a worker's role. Clearly, this condition can never be met! If, however, the mother should die (thereby setting $d_m = 1$), then one daughter should stay if $r^* = 0.5$. As r^* increases, more daughters are favored to stay (Fig. 1). This increase in helpers could represent the beginnings of a eusocial system, but it occurs only because haplodiploidy can produce $r^* > 0.5$.

The above example examines the head start hypothesis under the simplest condition of $s = (1 - d_w)$. It is more probable that daughter survivorship would be higher on her natal nest than if she left it, both because it is a favorable site and because no new nest need be built. Therefore, s must actually be less than 0.057, but there are not enough data for a reliable estimate. Moreover, *P. exclamans* is already eusocial, resulting in daughters that are more 'worker-like' and limited in their reproductive capabilities than could be expected in their non-eusocial ancestors. To simulate more likely ancestral states, I start with the assumption that all

females are 'queen-like' with a mortality rate of $d_m = d_w = 0.36$ (= the mortality rate of spring foundresses in *P. exclamans*) if they remain on their natal nest after emergence. Using Eqs 2–4, the number of daughters that should stay on the natal nest for given r^* values is predicted if the mortality rate for initiating a new nest is 2–20 times greater than that for remaining (Fig. 1).

There are two significant results. First, even when solitary founding is 20 times more dangerous than remaining, no more than 4 females should ever occupy the same nest at the same time. The benefit they provide in helping their parent does not exceed the fitness gained in attempting to nest on their own. Second, there is great selective pressure for at least one female to always remain on the nest. This means that if the mother should die, one daughter should assume parenting even if her relatedness to the remaining offspring is no more than that of a half-sib. An additional factor favoring at least one daughter to remain at the nest is that her presence would allow the foundress to stop foraging. Her continual presence on the nest would guard against brood parasites and predators. Not foraging would also decrease the foundress's mortality rate (d_m). Therefore, s^* may be underestimated in the model presented here for the first wasps to join. However, although enhanced brood protection may select for increased cooperation by 2–3 wasps, guarding benefits appear to also have rapidly diminishing returns with increasing number of wasps (see Strassmann et al. 1988), and thus cannot explain larger aggregations in a head start context.

Implications about the evolution and behaviour of eusocial Hymenoptera

Queller's (1989) initial formulation of the reproductive head-start hypothesis suggested that offspring dependence was of far greater importance in evolution of eusociality than haplodiploidy. Gadagkar's (1990) modifications to the model reduced the apparent head-start advantage, but he also concluded that worker behaviour was likely to evolve because of its assured fitness returns. However, both models implicitly require linear returns per unit effort – that is, a given amount of working always accrues the same fitness, independent of the number of wasps on a nest. If this assumption is relaxed such that each additional wasp that stays on the natal nest, increases survivorship proportionally less, then the head-start advantage by itself cannot explain why groups of five or more wasps should ever cooperate on a single nest.

Nevertheless, the head start could be a contributing factor in producing situations conducive for the future evolution of true eusociality. The model as modified here, does predict that cooperation between 2–4 wasps is possible, particularly if, due to haplodiploidy, relatedness among nestmates is high. This presents an opportu-

nity for selection on any mutualistic interactions (Lin and Michener 1972) that could further enhance nest success so that b^* exceeds b , and could produce a positive feedback loop eventually resulting in eusociality. Parental manipulation of daughters into becoming obligate workers (Alexander 1974) may also be more likely to evolve when reproductively capable daughters are already facultatively adopting worker roles.

Such facultative joining behaviour in daughters is consistent with the phylogeny of the social Vespidae. Carpenter (1989) proposes that a rudimentary caste-containing stage is the intermediate step between solitary living and eusociality, with reproductive division of labor evolving simultaneously with nest sharing.

The model presented here shares one conclusion with Queller's and Gadagkar's models: that it is extremely advantageous for one wasp to always remain on a nest containing brood, even if that brood is but distantly related. Queller and Gadagkar phrased this advantage in the context of nestmates taking care of each other, but the models need not be thus restricted. Any orphaned colony should be a potential adoptee for wasps from other nests if the original foundresses had philopatric tendencies (Klahn 1979, Queller and Strassmann 1988). Furthermore, such alloparental care (cf. Wilson 1975) could evolve with moderate to low levels of relatedness easily achieved in both haplodiploid and diploid species.

However, neither should all nests be equally attractive for joining, nor should all offspring within a nest be equally valuable for raising. Older larvae or pupae should be more likely to be adopted because they require less time and effort to bring to maturity, making workers' assurance of fitness returns (sensu Gadagkar 1990) higher (i.e., with young larvae or eggs, workers may not survive the entire brood development period and must depend on others completing the task). Therefore, if relatedness is equal, adult wasps should preferably join or adopt older (in terms of average brood age) nests and once on a nest, should show preferential treatment of older larvae. The latter prediction would further suggest that if the original foundress dies, a worker should replace her eggs or young larvae with her own offspring.

Implications for diploid species

Queller concluded that head starts are so advantageous that haplodiploidy may play only a small part in social evolution, which led him to ask "why has eusociality evolved so few times?" (p. 3226). As I argue here, his parallel with diploid animals may be faulty on this point. The correct question may be: if the head start hypothesis so strongly predicts adoption or alloparental care towards distantly related young in wasps, is there a similar phenomenon amongst diploids? The answer

would appear to be yes. Riedman (1982) found examples of alloparental care or outright adoption in over 270 species of mammals and birds. Some of these cases were clearly kin selected, with individuals helping close genetic relatives, but kin selection was discounted in many cases where relatedness appeared to be low. The reproductive head-start hypothesis, however, would suggest that high relatedness is not a necessary precondition for adoption if the alloparent's survival probability until the adoptee reaches independence is high relative to the probability of surviving until its own next offspring reaches independence. Furthermore, the head-start hypothesis predicts the likelihood of alloparental care to increase with offspring age because of increasingly assured fitness returns.

Clearly not all cases of adoption increase the alloparent's fitness, such as in black-legged kittiwakes where the adopted chick survives at the expense of the parents' own genetic offspring (Pierotti and Murphy 1987). If adopted offspring are siblicidal, then initially accepting them has to be considered a reproductive mistake by the adults (Mock 1984). However, once presented with a fait accompli, the head-start hypothesis would predict that the best option left for the parents may be not to abandon the siblicide, but to raise it.

In conclusion, many diploid and haplodiploid species may share an evolutionary potential for cooperative breeding that involves a few, perhaps distantly related, kin. However, the further development of truly eusocial societies with a large number of individuals sacrificing direct reproduction appears to occur commonly only in haplodiploid Hymenoptera. Clearly there must be unique selection pressures on the Hymenoptera that compliment the head-start advantage in producing this higher degree of sociality.

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References

- Alexander, R. D. 1974. The evolution of social behavior. – *Ann. Rev. Ecol. Syst.* 5: 325–383.
- Carpenter, J. M. 1989. Testing scenarios: wasp social behavior. – *Cladistics* 5: 131–144.
- Gadagkar, R. 1990. Evolution of eusociality: the advantage of assured fitness returns. – *Phil. Trans. R. Soc. Lond. B* 329: 17–25.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. – *J. Theor. Biol.* 7: 1–52.
- Klahn, J. E. 1979. Philopatric and nonphilopatric foundress associations in the social wasp *Polistes fuscatus*. – *Behav. Ecol. Sociobiol.* 5: 417–424.
- Lin, N. and Michener, C. D. 1972. Evolution of sociality in insects. – *Quart. Rev. Biol.* 47: 131–159.
- Michener, C. D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. – *Insectes Soc.* 11: 317–342.
- Mock, D. W. 1984. Infanticide, siblicide, and avian nesting mortality. – In: Hausfater, G. and Hrdy, S. B. (eds), *Infanticide: comparative and evolutionary perspectives*. Aldine Press, New York, pp. 3–30.
- Pierotti, R. and Murphy, E. C. 1987. Intergenerational conflicts in gulls. – *Anim. Behav.* 35: 435–444.
- Queller, D. C. 1989. The evolution of eusociality: reproductive head starts of workers. – *Proc. Natl Acad. Sci.* 86: 3224–3226.
- and Strassmann, J. E. 1988. Reproductive success and group nesting in the paper wasp, *Polistes annularis*. – In: Clutton-Brock, T. (ed.), *Reproductive success: studies of individual variation in contrasting breeding systems*, Univ. of Chicago Press, Chicago, pp. 76–96.
- Riedman, M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. – *Quart. Rev. Biol.* 57: 405–435.
- Strassmann, J. E., Queller, D. C. and Hughes, C. R. 1988. Predation risk and the evolution of sociality in the paper wasp *Polistes bellicosus*. – *Ecology* 69: 1497–1505.
- Wilson, E. O. 1975. *Sociobiology* – Harvard Univ. Press, Cambridge, MA.