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# Extended parental care and the origin of eusociality

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## SUMMARY

Eusocial insects are striking both for their enormous ecological success and for the unusual reproductive altruism of their workers. An explanation for both may lie in the advantage of providing extended care of the young. In insects, a single adult lifetime is often too short to allow extended care of the young. However, groups of adults can successfully provide overlapping care even if individual lifetimes are short, and the resulting high offspring survivorship may help account for the ecological success of social insects compared with solitary competitors. Models developed here show that the same advantage may have been a major selective force at the origin of eusociality.

## 1. INTRODUCTION

Eusocial insects are defined by overlap of adult generations, cooperative brood care, and reproductive division of labour (Wilson 1971). They pose both an ecological and an evolutionary problem. The ecological puzzle is why they are so successful (Wilson 1990), constituting 75% of the insect biomass in some ecosystems (Fittkau & Klinge 1973). The evolutionary puzzle concerns the reproductive division of labour: why should some individuals give up their own reproduction?

Hamilton (1964*a, b*) provided the framework for addressing the evolutionary problem. He showed that selection favours reproductive altruism when  $rB > \frac{1}{2}C$ , or

$$B/C > 1/(2r). \quad (1)$$

Here  $C$  is the fitness cost to the altruist and  $B$  the gain to the beneficiary, and  $r$  and  $\frac{1}{2}$  are the altruist's relatedness to the beneficiary's offspring and to its own offspring. Two classes of explanations of the evolution of eusociality emerge from Hamilton's rule. First, eusociality might be favoured if  $r > \frac{1}{2}$ , which is possible for haplodiploid organisms such as ants, wasps and bees, in which full sisters are related by  $3/4$  (Hamilton 1964*a, b*). Second,  $B$  could be sufficiently larger than  $C$  to compensate for any relatedness disadvantage, but this requires an explanation of how a helper can give more to her queen than to herself. Perhaps some individuals are physiologically equipped to be workers but not queens (subfertility) (West-Eberhard 1978). Alternatively, individuals working together might be able to organize their tasks more efficiently (Oster & Wilson 1978). None of these explanations readily links the evolutionary cause of eusociality with its ecological success. Neither haplodiploidy nor subfertility generates any obvious ecological advantage. Efficient task organization could be a reason for ecological success (Oster & Wilson 1978), but most such efficiencies

must have been selected after eusociality evolved (for an exception, see Wenzel & Pickering 1991).

A largely overlooked advantage stems from the ability to provide extended parental care. Parental care is recognized as an important pre-condition for eusociality because it means that there are dependent young, pre-existing abilities to provide care, the potential for overlap of generations, and asymmetries of both power and relatedness favouring parental control (Alexander 1974; Charnov 1978; Alexander *et al.* 1991). But it can also generate a special selective force in favour of helping behaviour. If offspring require extended care, but adults risk high mortality, then a large fraction of independently nesting adults will fail to raise any young (Queller 1989; Strassmann & Queller 1989). Suppose all adults suffer mortality at instantaneous rate  $q$  and, after investing for time  $T$ , their investments begin maturing at rate  $m$ . A female beginning a new nest has expected success

$$\int_T^\infty m e^{-qt} dt = (m/q) e^{-qT}.$$

The  $e^{-qT}$  term reflects the investment wasted when death of the adult leaves offspring unattended. Workers in fully eusocial colonies can avoid this kind of waste, either by completing the investments of others (Queller 1989; Strassmann & Queller 1989) or by having their investments carried through by others (Strassmann & Queller 1989; Gadagkar 1990). Even when workers have high mortality, they are able to carry offspring to independence through the overlap of adult lifetimes.

However, it is not obvious that eusociality could begin in this way. Specifically, how was the first helper able to do anything before time  $T$ , in addition to what the foundress would have done anyway? That is, if one member of the pair dies, how can the other member carry forward its incomplete investments without giving up an equivalent amount of other investments it would have made? Below I describe six distinct ways that this can occur.

## 2. THE MODEL

Inclusive fitness is a reasonable guide to the evolution of sterility if we assume sterility alleles with low penetrance or conditional expression (Charlesworth 1980; Grafen (1985). Let  $t = 0$  be the time when an adult female must choose whether to nest alone or help the foundress on her natal nest (usually her mother, but possibly another relative). The benefit:cost ratio for a helper in a population of non-helpers can be written as follows:

$$B/C = (F_{\text{both}} + F_{\text{found}} + F_{\text{helper}} - \int_0^{\infty} m e^{-qt} dt) / (\int_T^{\infty} m e^{-qt} dt - H_{\text{helper}}). \quad (2)$$

The benefit to the foundress is the additional offspring she gets because of help. The first three  $F$  terms sum up the number of foundress offspring who become independent when: (i) both the foundress and helper are alive; (ii) when only the foundress is still alive, and (iii) when only the helper is still alive. The net benefit of helping is obtained by subtracting the offspring the foundress would produce if she were not helped. The cost to the helper is the number of offspring she would have reared alone (starting at time  $T$ ) minus the number of her own offspring she rears if she helps ( $H_{\text{helper}}$ ). I will assume throughout that the helper lays no eggs until the foundress dies.

First consider the case in which the foundress continues to care for her own young at the same rate, but also begins providing the helper with a separate set of eggs to tend. Each cares for only its own set of foundress eggs, even if the other adult dies. This base model is artificial (why wouldn't they both care for the combined set of eggs?), but it serves two purposes. First, it should be evident that, with separate care, there is no net gain to helping. The helper must still survive to time  $T$  to rear any of her set of foundress young to independence, the same as if she nested alone. Therefore, the base model sets a standard against which proposed advantages can be compared, one at a time. The base model also serves as an introduction to the formalization necessary for more complicated cases. In each model, we will need to write expressions for the parameters of equation (2) ( $F_{\text{both}}$ ,  $F_{\text{found}}$ ,  $F_{\text{helper}}$ ,  $H_{\text{helper}}$ ). The expressions for the base model are given in the first row of table 1. The limits of the integrals over time ( $t$ ) are the times when young become independent, and the integration is over the rate of gain ( $m$ , or, if both survive past time  $T$ ,  $2m$ ) times the probability of survival to realize these gains ( $e^{-2qt}$  for two adults,  $e^{-qt}$  for one). For gains after the helper dies, this integral is embedded within another that gives the time distribution of helper death ( $\int_0^{\infty} q e^{-qt} dt$ , where  $t_h$  is the time of helper death). A parallel form is used for the time of foundress death,  $t_f$ . If equation 1 is solved by using the base model terms,  $B/C = 1$ , as expected. There is no advantage if the helper simply tends a separate set of the queen's young.

At least six advantages can alter this conclusion. The simple verbal descriptions given below are formalized mathematically in table 1 to give an idea of the magnitude of the helping advantage. Some advantages

can be combined, but each is treated alone so its individual effects can be seen. Graphs of the  $B/C$  ratios for selected parameter values appear in figure 1, plotted as functions of adult mortality before offspring can be reared to independence ( $1 - e^{-qt}$ ).

(a) *Model 1. Deteriorating conditions*

Suppose the foundress has begun her nest under good conditions, and she has invested for time  $T$  on the assumption that she can rear young at rate  $km$  ( $k > 1$ ). Then conditions deteriorate so that she can only rear at rate  $m$ . A helper can begin rearing the extra young immediately (Queller 1989) (but cannot more than double the foundress's rate even if  $k > 2$ ).

(b) *Model 2. Adoption*

Instead of staying with her separate set of foundress progeny when the foundress dies, the helper can adopt the other set if they are more advanced in age (Nonacs 1991). This means she can always begin rearing extra independent young at time  $t_f$ .

(c) *Model 3. Foundress mortality reduction*

Assume that when a helper joins, the foundress stops working (except to provide eggs), reducing her mortality rate to zero until after the worker dies and she must resume work. The worker carries on the foundress's investments, and she may even be forced by the foundress to work as hard as two normal individuals. Assume that a helper working  $d$  times harder than usual increases her mortality rate to  $dq$  and increases her productivity (in rearing foundress young) from  $m$  to  $dm$  once she survives past time  $T$ . In effect, the helper intercalates her adult lifetime into that of the foundress, taking over the foundress's investments, and letting the foundress survive to eventually take over hers. Of course, this advantage is lower if foundress mortality is not reduced all the way to zero, but it can still be substantial.

Although this advantage can be large, it is not optimal by itself. With model 3 alone, helping is inferior (if  $r < \frac{1}{2}$ ) to the alternative strategy of reducing one's own mortality to zero by not working, but monitoring the natal nest to take it over when the foundress dies. However, it could be superior when coupled with model 5 or other non-demographic advantages.

Three additional models work if offspring require different kinds of care at different stages, with only one kind being limiting. Suppose provisioning of larvae limits the number of offspring that can be reared. Defence of young at other stages may be important but not limiting. A bee guarding the nest entrance, or a wasp applying ant repellent to her nest pedicel, can protect many young as easily as one. In the models that follow, assume that provisioning of an offspring begins after  $aT$  units of time and ends after  $bT$  units. Figure 2 shows some possible forms of investment for a progressive provisioner and a mass provisioner.

Table 1. Benefits and costs of helping for models described in the text

('Base value' refers for the corresponding expression in the base model in the first row. All integrals can be solved by using  $\int_{t_1}^{t_2} x e^{-yt} dt = (x/y)(e^{-yt_1} - e^{-yt_2})$ , where  $x$  and  $y$  are any constants. For any model, substitution of the first four entries into equation (2) yields the benefit:cost ratio in the last column.)

Model	$F_{\text{found}}$	$F_{\text{both}}$	$F_{\text{helper}}$	benefit/cost
Base model: separate care	$\int_0^T m e^{-2yt} dt + \int_T^\infty 2m e^{-2yt} dt$	$\int_0^\infty q e^{-yt} dt + \int_{t_h}^\infty m e^{-yt} dt dt_h$	1	
1. Deteriorating conditions	$\int_0^T km e^{-2yt} dt + \int_T^\infty 2m e^{-2yt} dt$	base value	$\int_0^\infty q e^{-yt} dt + \int_{t_1+T}^\infty m e^{-yt} dt dt_t$	$[e^{-kt} + (k-1)(1 - e^{-2yt})]/e^{-yt}$
2. Adoption	base value	base value	base value	$(1 + e^{-2yt} - e^{-yt})/e^{-yt}$
3. Foundress mortality reduction	$\int_0^T m e^{-yt} dt + \int_T^\infty dm e^{-at} dt$	$\int_0^\infty dy e^{-yat} dt + \int_{t_h}^\infty m e^{-yt-t_h} dt dt_h$	0	$\{1 + (d-1) e^{-at}\}/(de^{-at})$
4. Follow-up defence	base value	base value + $\int_{t_h}^T q e^{-yt} dt + \int_T^\infty m e^{-yt} dt dt_h + \int_{t_h}^\infty q e^{-yt} dt dt_h$	base value	$(3 - 3e^{-at} + 3e^{-2at} + 2e^{-at} - 2e^{-a(3-b)t})/(3e^{-at})$
5. Extra inexpensive eggs	$\int_0^{T-aT} m e^{-2at} dt + \int_{T-aT}^\infty 2m e^{-2at} dt$	base value	base value	$(2e^{-a(T-aT)} - e^{-aT})/e^{-aT}$
6. Feed larvae while tending inexpensive eggs	base value + $\int_{T-bT}^{T-aT} cm e^{-2at} dt$	base value + $\int_0^T q e^{-at} dt + \int_{T-bT}^\infty cm e^{-at} dt dt_h + \int_{T-bT}^\infty q e^{-at} dt dt_h$	base value + $\int_0^T q e^{-at} dt + \int_{T-bT}^\infty cm e^{-at} dt dt_h + \int_{T-bT}^\infty q e^{-at} dt dt_h$	$[e^{-at} + ce^{-a(1-b)T}(1 - e^{-2aT})]/e^{-aT}$
model	$F_{\text{found}}$	$F_{\text{both}}$	$F_{\text{helper}}$	benefit/cost
Base model: separate care	$\int_0^T q e^{-yt} dt + \int_T^\infty m e^{-yt} dt dt_t$	$\int_0^T m e^{-2yt} dt + \int_T^\infty 2m e^{-2yt} dt$	$\int_0^\infty q e^{-yt} dt + \int_{t_1+T}^\infty m e^{-yt} dt dt_t$	1
1. Deteriorating conditions	base value	base value	base value	
2. Adoption	$\int_0^\infty q e^{-yt} dt + \int_{t_1+T}^\infty m e^{-yt} dt dt_t$	base value + $\int_{bT}^{2bT} q e^{-at} dt + \int_T^\infty m e^{-at} dt dt_t + \int_T^\infty q e^{-at} dt dt_t$	base value	
3. Foundress mortality reduction	base value	base value + $\int_{bT}^{2bT} q e^{-at} dt + \int_T^\infty m e^{-at} dt dt_t + \int_T^\infty q e^{-at} dt dt_t$	base value	
4. Follow-up defence	base value + $\int_{bT}^{2bT} q e^{-at} dt + \int_T^\infty m e^{-at} dt dt_t + \int_T^\infty q e^{-at} dt dt_t$	base value	base value	
5. Extra inexpensive eggs	base value + $\int_{bT}^{2bT} q e^{-at} dt + \int_T^\infty m e^{-at} dt dt_t + \int_T^\infty q e^{-at} dt dt_t$	base value	base value	
6. Feed larvae while tending inexpensive eggs	base value + $\int_{bT}^{2bT} q e^{-at} dt + \int_T^\infty m e^{-at} dt dt_t + \int_T^\infty q e^{-at} dt dt_t$	base value	base value	

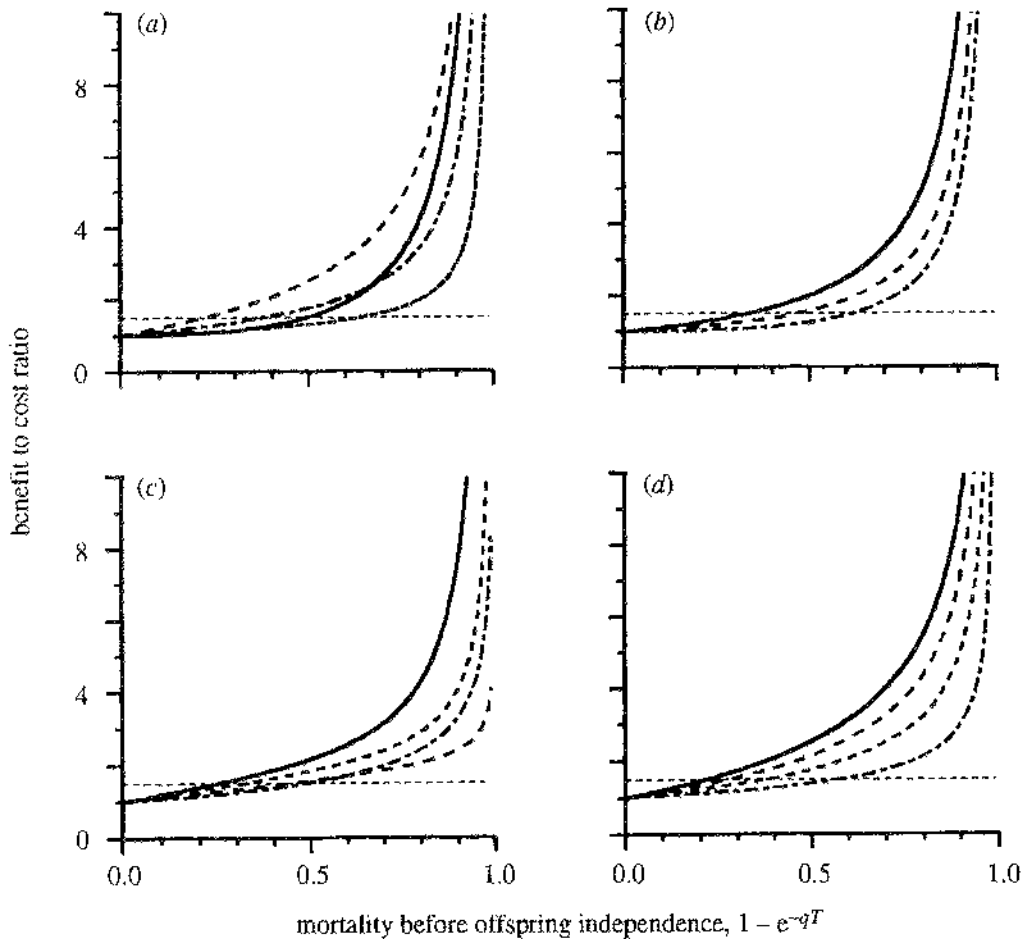


Figure 1. Selected benefit/cost ratios for the models in table 1. Helping behaviour is favoured if the reciprocal of the benefit/cost ratio exceeds the helper's relatedness to the offspring helped. For comparison, the horizontal broken line at 1.5 represents the advantage generated by aiding haplodiploid full sisters ( $r = \frac{3}{4}$ ) instead of offspring ( $r = \frac{1}{2}$ ), when  $B = C$ . (a) Model 1,  $k = 2.0$  (dashed line),  $k = 1.5$  (dot-dash line),  $k = 1.2$  (broken line); model 2 (solid line). (b) Model 3,  $d = 1.0$  (solid line),  $d = 1.5$  (dashed line),  $d = 2.0$  (dot-dash line). (c) Model 4,  $b = 0$  (solid line),  $b = \frac{1}{3}$  (broken line),  $b = \frac{2}{3}$  (dashed line); model 5,  $a = \frac{1}{3}$  (dot-dash line). (d) Model 6,  $a = \frac{1}{3}$ ,  $b = \frac{2}{3}$ , and  $c = 1$  (solid line),  $c = 0.75$  (dashed line),  $c = 0.5$  (broken line),  $c = 0.25$  (dot-dash line).

(d) *Model 4. Follow-up defence*

Once offspring reach age  $bT$ , they may be immune to orphaning by the death of only one adult. The surviving adult can defend them at no extra cost while continuing to provide for its 'own' set of young (Lin & Michener 1972). If the first adult to die does so after time  $bT$ , the survivor continues rearing the provisioned young for time  $T - bT$ ,  $t_1 - bT$ , or  $t_n - bT$ , whichever is shortest.

(e) *Model 5. Extra inexpensive eggs*

If tending eggs is inexpensive, as in the progressive provisioning scenario of figure 2, the foundress may often lay extra eggs, allowing the helper to aid by feeding the resulting extra larvae. Initially this might occur as bet-hedging strategy, with the foundress laying extra eggs on the chance that conditions will improve and she will be able to rear more. Once eusociality has evolved, the foundress might provide extra eggs on the expectation of future help. Either way the helper gets a head start of  $aT$  time units on when she starts contributing. This shortens the period when

two-adult colonies produce at rate  $m$  instead of  $2m$ , and also the period when the helper is left without nearly mature young after the death of the foundress.

(f) *Model 6. Feed larvae while tending inexpensive eggs*

Now suppose that the foundress provides extra eggs only after the helper's arrival. A helper with only newly laid eggs to tend has little to do until they hatch. She can therefore devote effort before time  $aT$  to feeding the foundress's larvae. These were already being provisioned by the foundress, but it is still likely that they could benefit to some degree from extra feeding. If the helper's feeding of late-stage larvae (age  $bT$ ) increases their fitness by an amount  $c$ , the helper begins contributing at rate  $cm$  when the aided larvae begin to reach independence at time  $T - bT$ . This continues for time  $aT$ ,  $t_n$  or  $t_r$ , whichever is shortest. This advantage is not available to solitary females because they have no larvae to feed before time  $aT$ .

The graphs of benefit:cost ratios for each model plotted in figure 1 show that the advantages proposed here can be large. In each case, if there is no adult mortality,  $B/C = 1$ . But any mortality at all pushes the

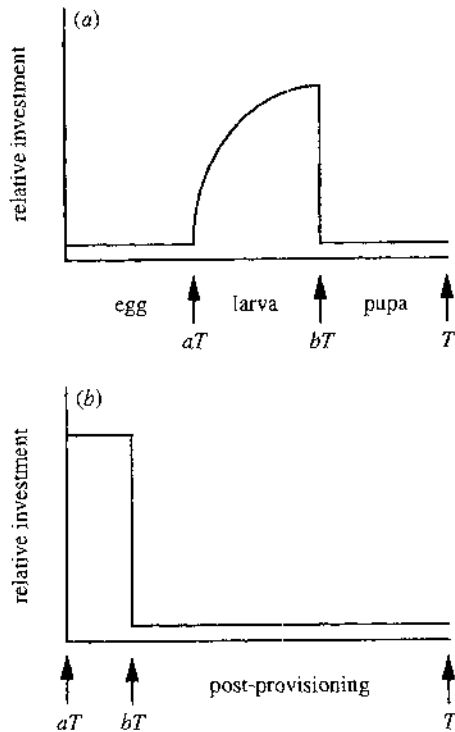


Figure 2. Schematic representation of the relative amounts of investment required by young of various stages, for (a) a progressive provisioner and (b) a mass provisioner.  $T$  is the time when offspring become independent; provisioning begins at time  $aT$  and ends at  $bT$ .

$B/C$  ratio above 1, which is enough to select for helping if  $r = \frac{1}{2}$ . At moderate to high mortality rates, the advantages can become far greater than the maximum advantage possible through the haplodiploid hypothesis (horizontal lines at 1.5). Sociality could even evolve under rather low relatedness. For example, a  $B/C$  value of 4 would allow sociality for any  $r > \frac{1}{3}$  (see equation (1)). Some of the separate advantages could apply at the same time, further increasing  $B/C$ . Other combinations are incompatible. Of course, these  $B/C$

ratios include only the demographic factors specified for each model. In reality, the advantages may need to be greater to overcome other disadvantages that usually attend living in groups (Alexander 1974).

### 3. DISCUSSION

Clearly, large advantages to helping can be obtained provided there is significant adult mortality. Colonies initiated by single females give a rough idea of the kinds of mortality rates that might have applied at the origin of eusociality. Table 2 lists single-foundress failure rates before the emergence of their first adult brood for 14 species (17 studies) of polistine wasps lacking morphological castes. I do not claim that these social species exactly match the assumptions of the model, but clearly solitary foundresses suffer sufficient mortality to make substantial advantages to helping possible (figure 1). Moreover, there are two reasons why these rates may be lower than those of the incipiently eusocial ancestors of these species. First, there is a very high payoff to these females if they survive to have helpers, so they may be more conservative in taking risks than females in a species with no evolutionary history of helping. Secondly, those females choosing to found nests alone when there are other alternatives may be those that have the best survival prospects. Average mortality is even higher for workers (Queller 1989; Gadagkar 1990). Comparable data on survivorship of solitary species would be of considerable interest.

Apart from sociality itself, perhaps the most exceptional feature of eusocial insect species is the length and importance of the care given to the young (Alexander *et al.* 1991). This could simply be because of the importance of parental care in setting the stage for helping. However, the models developed here suggest a deeper link. The advantages of extended parental care can be realized most consistently if care givers group

Table 2. Failure rates of single foundresses before the emergence of their first adult young

species	failure rate (%)	number of colonies	reference
<i>Mischocyttarus mexicanus</i>	38	76	Little (1977, 1979)
<i>Polistes fuscatus</i>	40	277	Klahn (1981) and J. E. Klahn (personal communication) in Hughes (1987)
<i>Mischocyttarus flavitarsus</i>	45	73	Little (1979)
<i>Polistes fuscatus</i>	47	55	Noonan (1979)
<i>Polistes chinensis</i>	49	230	Miyano (1980)
<i>Polistes jadvigae</i>	53	90	Matsuura (1977), cited in Miyano (1980)
<i>Polistes biglumis bimaculatus</i>	58	24	Lorenzi & Turillazzi (1986)
<i>Polistes chinensis</i>	60	421	Matsuura (1977), cited in Miyano (1980)
<i>Ropalidia fasciata</i>	61	109	Itô (1993)
<i>Polistes nimpha</i>	68	37	Turillazzi (1984)
<i>Polistes riparius</i>	71	63	Yamane & Kawamichi (1975), cited in Hughes (1987)
<i>Mischocyttarus labiatus</i>	80	20	Little (1981, 1979)
<i>Polistes annularis</i>	80	72	Strassmann (1989)
<i>Polistes snelleni</i>	84	38	Yamane (1969), cited in Hughes (1987)
<i>Polistes fuscatus</i>	93	45	Gibo (1978)
<i>Polistes canadensis</i>	97	143	Pickering (1980), tabulated in Hughes (1987)
<i>Belonogaster petiolata</i>	100	38	Keeping & Crewe (1987)

together to ensure against the risks of high adult mortality rates.

These models treated the simplest case in which offspring depend absolutely on extended care to survive to independence. If they are viewed too literally, one might falsely conclude that the advantages described apply only to escaping an extraordinarily feeble ancestral mode of life in which solitary individuals tried to provide extended care, but usually failed to reproduce at all. But the kinds of advantages developed here still apply, although with somewhat less force, if offspring sometimes survive being orphaned but survive better with more extended care. Perhaps the absolute dependence evolved after eusociality provided some assurance that offspring could receive extended care.

Regardless of whether absolute offspring dependence preceded or followed eusociality, it is important to realize that the true advantage described here is high offspring survival. Eusocial groups are more productive because they can provide enough care to attain high offspring survival. This can easily provide an ecological advantage, either over solitary species that try to provide extended care but often fail because of adult mortality, or over solitary species that do not provide extended care and suffer the consequence of low offspring survivorship. Solitary founding in eusocial species reduces this ecological advantage but does not eliminate it because it still applies to the post-founding stages of the colony cycle.

Thus, to a large extent, the evolutionary and ecological puzzles posed at the beginning of this paper may have the same solution. Social groups can effectively provide extended parental care and attain high offspring survivorship, and the models developed here show how this advantage could have driven the origin of sociality. Although the ecological dominance of social insects surely stems in part from efficiencies selected after sociality evolved, much of it may derive from the same advantage that caused eusociality to evolve in the first place.

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## REFERENCES

- Alexander, R. D. 1974 The evolution of social behaviour. *A. Rev. Ecol. Syst.* 5, 325–383.
- Alexander, R. D., Noonan, K. M. & Crespi, B. J. 1991 The evolution of eusociality. In *The biology of the naked mole rat* (ed. P. W. Sherman, J. U. M. Jarvis & R. D. Alexander), pp. 3–44. Princeton University Press.
- Charlesworth, B. 1980 Models of kin selection. In *Evolution of social behaviour: hypotheses and empirical tests* (ed. H. Markl), pp. 11–26. Weinheim: Verlag Chemie.
- Charnov, E. 1978 Evolution of eusocial behaviour: offspring choice or parental parasitism. *J. theor. Biol.* 75, 451–465.
- Fittkau, O. H. & Klinge, H. 1973 On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* 5, 2–14.
- Gadagkar, R. 1990 Evolution of eusociality: the advantage of assured fitness returns. *Phil. Trans. R. Soc. Lond. B* 329, 17–25.
- Gibo, D. L. 1978 The selective advantage of foundress associations in *Polistes fuscatus* (Hymenoptera: Vespidae): a field study of the effects of predation on productivity. *Can. Entomol.* 110, 519–540.
- Grafen, A. 1985 A geometric view of relatedness. *Oxf. Surv. Evol. Biol.* 2, 28–89.
- Hamilton, W. D. 1964a The genetical evolution of social behaviour. I. *J. theor. Biol.* 7, 1–16.
- Hamilton, W. D. 1964b The genetical evolution of social behaviour. II. *J. theor. Biol.* 7, 17–52.
- Hughes, C. R. 1987 Group nesting and reproductive conflict in primitively eusocial wasps. Unpublished Ph.D. thesis, Rice University, Houston.
- Itô, Y. 1993 *Behaviour and social evolution of wasps*. Oxford University Press.
- Keeping, M. G. & Crewe, R. M. 1987 The ontogeny and evolution of foundress associations in *Belonogaster petiolata* (Hymenoptera: Vespidae). In *Chemistry and biology of social insects* (ed. J. Eder & H. Rembold), pp. 383–384. Munich: J. Peperny.
- Klahn, J. E. 1981 Alternative reproductive tactics of single foundresses of a social wasp, *Polistes fuscatus*. Unpublished Ph.D. thesis, University of Iowa.
- Lin, N. & Michener, C. D. 1972 Evolution of sociality in insects. *Q. Rev. Biol.* 47, 131–159.
- Litte, M. 1977 Behavioural ecology of the social wasp, *Mischocyttarus mexicanus*. *Behav. Ecol. Sociobiol.* 2, 229–246.
- Litte, M. 1979 *Mischocyttarus flavitarsus* in Arizona: social and nesting biology of a polistine wasp. *Z. Tierpsychol.* 50, 282–312.
- Litte, M. 1981 Social biology of the polistine wasp *Mischocyttarus labiatus*: survival in a Colombian rainforest. *Smithson. Contr. Zool.* 327, 1–27.
- Lorenzi, M. C. & Turillazzi, S. 1986 Behavioural and ecological adaptations to the high mountain environment of *Polistes biglumis bimaculatus*. *Ecol. Ent.* 11, 199–204.
- Matsuura, M. 1977 Life of *Polistes* wasps. *Shizen* 32, 26–36. (In Japanese.)
- Miyano, S. 1980 Life tables of colonies and workers in a paper wasp, *Polistes chinensis antennalis*, in central Japan (Hymenoptera: Vespidae). *Res. Popul. Ecol.* 22, 69–88.
- Nonacs, P. 1991 Alloparental care and eusocial evolution: the limits of Queller's head start advantage. *Oikos* 61, 122–125.
- Noonan, K. M. 1979 Individual strategies of inclusive fitness maximizing in the social wasp, *Polistes fuscatus* (Hymenoptera: Vespidae). Unpublished Ph.D. thesis, University of Michigan.
- Oster, G. R. & Wilson, E. O. 1978 *Caste and ecology in the social insects*. Princeton University Press.
- Pickering, J. 1980 Sex ratio, social behavior and ecology in *Polistes* (Hymenoptera, Vespidae), *Pachysomoides* (Hymenoptera, Ichneumonidae) and *Plasmodium* (Protozoa, Haemsporidia). Unpublished Ph.D. thesis, Harvard University.
- Queller, D. C. 1989 The evolution of eusociality: reproductive head starts of workers. *Proc. natn. Acad. Sci. U.S.A.* 86, 3224–3226.
- Strassmann, J. E. 1989 Group colony foundation in *Polistes annularis* (Hymenoptera: Vespidae). *Psyche* 96, 223–236.
- Strassmann, J. E. & Queller, D. C. 1989 Ecological determinants of social evolution. In *The genetics of social evolution* (ed. M. D. Breed & R. E. Page, Jr), pp. 81–101. Boulder: Westview Press.
- Turillazzi, S. 1984 Defensive mechanisms in *Polistes* wasps. In *Defensive mechanisms in social insects* (ed. H. H. Hermann), pp. 33–58. New York: Praeger.

- Wenzel, J. W. & Pickering, J. 1991 Cooperative foraging, productivity, and the central limit theorem. *Proc. natn. Acad. Sci. U.S.A.* **88**, 36–38.
- West-Eberhard, M. J. 1975 The evolution of social behaviour by kin selection. *Q. Rev. Biol.* **50**, 1–33.
- Wilson, E. O. 1971 *The insect societies*. Cambridge, Massachusetts: Harvard University Press.
- Wilson, E. O. 1990 *Success and dominance in ecosystems: the case of the social insects*. Oldendorf/Luhe: Ecology Institute.
- Yamane, S. 1969 Preliminary observations on the life history of two polistine wasps, *Polistes snelleni* and *Polistes biglumis* in Sapporo, Northern Japan. *J. Fac. Sci. Hokkaido Univ. (Ser. 6)* **17**, 78–105.
- Yamane, S. & Kawamichi, T. 1975 Bionomic comparison of *Polistes biglumis* (Hymenoptera: Vespidae) in two different localities in Hokkaido, Northern Japan, with reference to its probable adaptation to cold climate. *Kontyû* **43**, 214–232.

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