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Nonacs, Peter

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Competition and kin discrimination in colony founding by social Hymenoptera

PETER NONACS*

Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

Summary

After mating, queens of social wasp and ant species sometimes band together to start a new colony cooperatively. I assume these queens sequentially encounter potential nest sites that may or may not already contain a queen. Whether to remain at a given site or to leave in hopes of finding a better site is modelled using dynamic programming. The results suggest that discriminating competitive ability is more valuable than discriminating kinship. Wasps, which have a high survival rate in transitions between nest site encounters and in which pleometrosis seems to have a consistently high benefit, are predicted to discriminate both competitive ability and kinship of potential partners. Ants, which have lower survivorship and variable benefits, are predicted to show conditional joining behavior (sometimes based on discriminating competitive ability, but almost never based on discriminating kinship). A survey of the literature supports the model with respect to the predictions on kin discrimination in both groups and on conditional joining behavior in ants. However, whether partners are joined based on perceptions of competitive ability needs more tests.

Keywords: Colony founding; competition; dynamic programming; Formicidae; Hymenoptera; kin discrimination; pleometrosis; Polistinae; social insects.

Introduction

Colonies of social Hymenoptera are often initiated by several queens cooperating to raise the first brood of workers (pleometrosis). This process has been studied extensively in temperate wasps (Polistinae) and ants. In both taxa, pleometrotic founding can produce mutualistic advantages for all the individual members of a group. Wasp foundresses hunt for prey and by having more foragers, groups can raise a larger first brood. This is a great advantage for annual species as early success can extend throughout the season into increased sexual production at the end of the life cycle (Gibo, 1978; Noonan, 1981; Strassmann, 1981a). Also, multiple foundresses are better at rebuilding nests destroyed by predators (Litte, 1977; Gamboa, 1978; Gibo, 1978; Strassmann, 1981b; Strassmann *et al.*, 1988). In ants, queens generally do not forage but raise the first brood from their own metabolic resources. Multiple foundresses can pool their resources and mature a larger first brood, more quickly in several species (Waloff, 1957; Bartz and Hölldobler, 1982; Rissing and Pollock, 1988).

Although pleometrosis may be of mutualistic benefit, not all individuals in a group share equally in the benefit. In wasps, one queen will usually dominate the egg-laying. The others will be eliminated or relegated to subordinate roles with reduced opportunities for reproduction

* Current address: Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA.

(Fletcher and Ross, 1985 and references within; Hughes and Strassmann, 1988). In ants, pleometrotic partners are eliminated by queen aggression or by the workers, so that in almost all cases only one of the original queens remains by the time the colony starts producing sexuals (Hölldobler and Wilson, 1977; Bartz and Hölldobler, 1982; Hölldobler and Carlin, 1985).

Differential survival and reproductive success suggests that queens should be selective about joining groups. By preferentially joining kin, gains in inclusive fitness could offset the possibility of lowered individual reproduction. Besides favoring kin, queens could also join groups based on the competitive abilities of the other queens. They may prefer groups in which they perceive their chances to gain control of reproduction to be favorable.

This paper models the decisions a queen faces in choosing a nest site in an environment where she encounters empty nest sites, nest sites containing kin or non-kin, and queens of variable competitive ability. The model compares how well simple nest site selection rules do in relation to optimal behavior. Finally, I compare general predictions from the model about wasp and ant queen pleometrotic behavior to observed behavior.

Methods

In this model, a queen has the possibility of nesting in five types of sites. A site can be empty or contain one of four categories of queens: full sisters ($G = 0.75$) or unrelated ($G = 0$) and, that are either good or poor competitors in eventually gaining control of reproduction. A queen's fitness in nesting alone is given a value of one. The fitness of nesting with a partner has a direct fitness component and, if the queen is kin, an inclusive fitness component. Direct fitness is a function of the queen's probability of gaining control of the colony (α) and the extra benefit (b) she inherits from pleometrosis. A queen's inclusive fitness component is negative if she eliminates kin and, if she is eliminated, it is the positive increase in her kin's direct fitness (both values are weighted by G). Therefore, a queen's average fitness in joining is:

$$\alpha(1 + b) - \alpha G + (1 - \alpha)Gb$$

rearranged to

$$\alpha(1 + b) + G(b - b\alpha - \alpha) \quad (1)$$

where α equals either 0.25 or 0.75 upon joining a good or poor competitor, respectively. Nesting with a queen is assumed to be beneficial by increasing colony success over nesting alone ($b > 0$). All queens are assumed to provide equal mutualistic benefit.

From Eqn (1) it is possible to rank the fitnesses of being with kin, non-kin or alone for any values of b and α . Depending on those values, there is always a 'best' type of nest site that should always be chosen with simultaneous presentations. However, it seems much more probable that sites are encountered sequentially. A queen encountering a less than optimal site, therefore, must decide whether to remain or find another nest site. If she goes on she may fall victim to predation, the elements, or next encounter a poorer site. If the next site is also non-optimal, the queen has to repeat the decision process. In essence, choosing a nest site for a Hymenoptera queen can be modelled as a decision process with multiple, sequential encounters.

Dynamic programming techniques are well suited for modelling repeated encounters. The methodology of constructing a dynamic optimization model is explained in detail in Houston *et al.* (1988) and Mangel and Clark (1988) and will only be abstracted here as it relates to pleometrosis.

Assume that a queen can encounter T nest sites in a given day or time period by the end of which she must be in a nest site or perish. The queen's optimal strategy is to maximize the fitness

function $J(x_i; T-n, T)$, when encountering nest site $T-n$ gives a queen a fitness of x_i . Therefore, at the last site ($n = 0$), the queen has no behavioral options. She must stay and her fitness function is $J(x_i, T, T)$ where x_i can assume one of five values: one if the site is empty, or if it contains a queen, a value determined by Eqn (1) depending on kinship, competitive ability and b . For any $T-n$ site ($n \geq 1$), queens can either stay or go on to the next site. The expected fitness of continued search is $\hat{x} \cdot s$ where $\hat{x}$ is the average fitness of the next site (calculated by summing all possible x_i at the next site, weighted by their frequency of encounter) and s is the survival rate between site locations ($0 < s \leq 1$). Therefore, if the queen always chooses the best option, her fitness function is determined as:

$$J(x_{i-5}, T-n, T) = \begin{cases} x_i (= \text{stay}) & \text{if } x_i > \hat{x} \cdot s \\ \hat{x} \cdot s (= \text{go}) & \text{if } x_i \leq \hat{x} \cdot s \end{cases} \quad (2)$$

for a given site encountered at a given time.

This type of modelling is also called backward induction because it works back from the terminal fitness function at the last site, T . By specifying fitnesses for all possible situations (x_i) at T , $\hat{x} \cdot s$ for $T-1$ can be calculated. This value is then compared to each x_i to determine the go–stay decision. If the queen leaves, $\hat{x} \cdot s$ replaces x_i as the expected fitness. Once fitnesses for all possible situations at $T-1$ are thus calculated, a new $\hat{x} \cdot s$ for $T-2$ can be determined. The process is continued through to the $T-n$ site. The model presented here is not state-dependent *sensu* Mangel and Clark (1988) because the searching queen's state does not change although her valuation of encountered patches does. The model is one of finding an optimal stopping point (DeGroot, 1970), by comparing the encountered situation to an estimated payoff of continued search. Previous applications, with dynamic programming techniques, have been used to estimate when foragers should stop feeding in a given patch (Green, 1984).

To model pleometrosis, it is necessary to assign frequencies to the encounters with site types. I initially assume that half of all the potential nest sites are empty. In the other half, kin or non-kin are equally likely to be encountered. Half the encountered queens are poor competitors and half are good competitors, with competitive ability identically distributed across kin and non-kin.

Conceptually, one can imagine behavioral decisions changing across nest site encounters as follows. At $T-1$, a queen that leaves a mediocre site could encounter a poorer one next and then be forced to stay there. A queen in a mediocre site at $T-10$ has at least 10 chances to improve herself and is not as likely to become trapped in a poorer site. Therefore, queens should be 'choosier' at $T-10$ than at $T-1$.

The above model assumes queens behave optimally by recognizing and responding correctly to the kinship and competitive ability of other queens, but does not determine how much better this is than simpler, but non-optimal rules of behavior. Therefore, I repeat the above calculations for queens that use a series of non-optimal rules.

The six simplest rules are unconditional, in that queen behavior is the same and independent of the values of s , b and $T-n$. They are: stay in any site encountered (= random site selection); stay only in empty sites; stay only with another queen; stay only with kin; stay only with non-kin; stay only with poor competitors.

Three more complex rules are conditional, in that the stay–go decisions are state dependent on the values of s , b and $T-n$. With Conditional Queen (C-Queen) queens can stay in empty and/or occupied sites based on the values in the inequalities in Eqn (2). Decisions are based on the fitness of joining the 'average' encountered queen with no discrimination of kinship or competitive ability. Similarly, Conditional Kin (C-Kin) lets queens stay in empty and/or occupied sites. Queens can discriminate between kin and non-kin, but not between poor and good

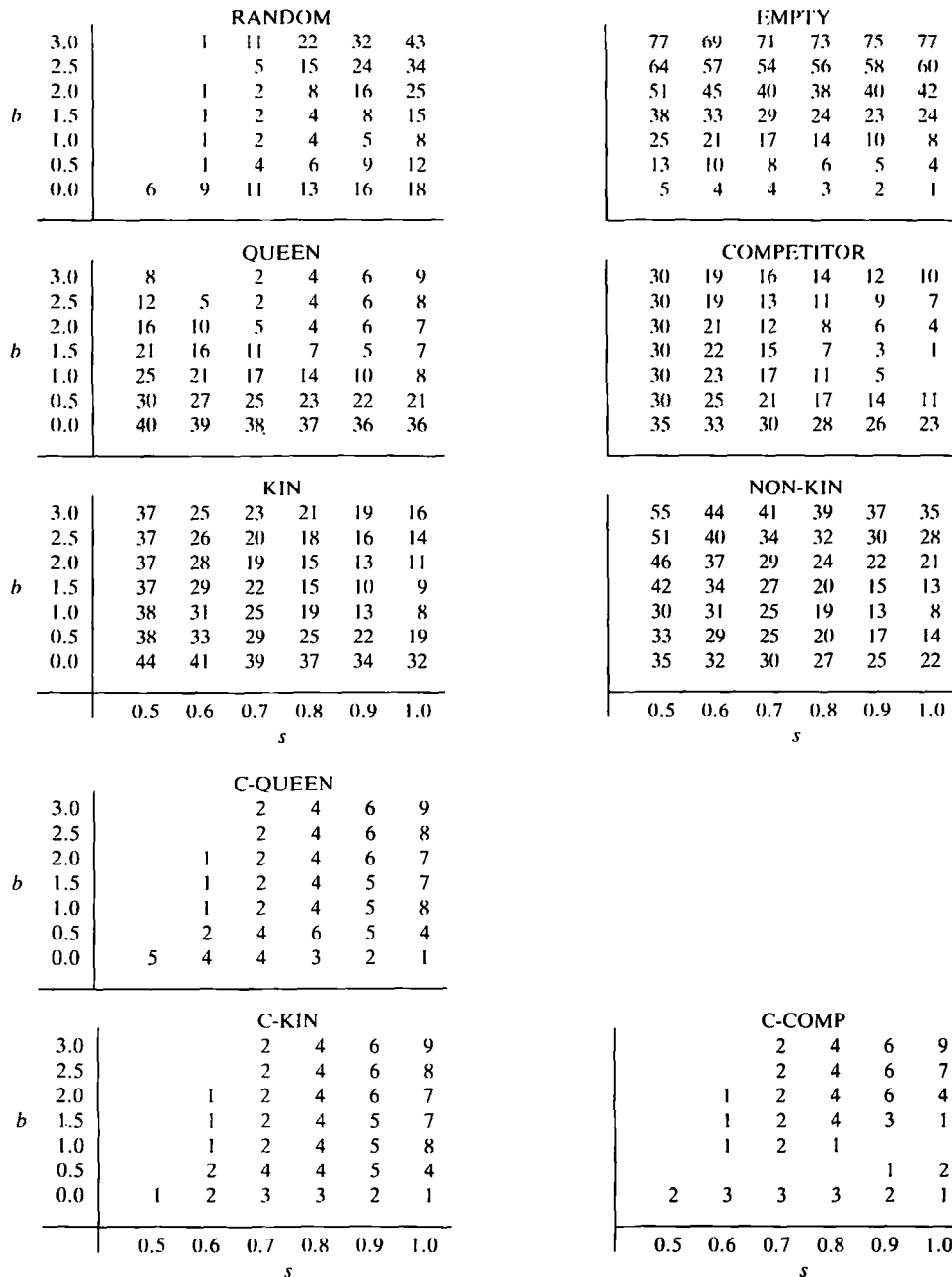


Figure 2. The percentage cost of using non-optimal decision rules at nest site $T-1$ for varying values of pleometrotic benefit (b) and survival rate while searching (s). The rules compared to optimality are: (1) random site selection (= stay at any site encountered); (2) stay only in empty sites; (3) stay only with a queen (but all queens are acceptable); (4) stay only with queens of poor competitive ability; (5) and (6) stay only with kin or non-kin, respectively; (7) stay in empty and/or occupied sites depending on the resultant fitness (C-Queen); (8) same as (7), but queens can discriminate between kin and non-kin (C-Kin); (9) same as (7), but queens can discriminate between good and poor competitors (C-Comp). Blanks indicate the rule is within 0.5% of optimal behavior.

almost as well as the $T-1$ nest site (Fig. 2). I define 'doing well' as resulting in a fitness that is within 10% of that achieved by being optimal. For example, the unconditional rule of stay at any site encountered (random) does well, except where both survival rate and benefits are high. Other unconditional rules have regions where they do approach optimal. When pleometrosis has little benefit ($b \leq 1$), staying only in empty sites does well. At higher bs , staying only with queens is the better strategy and close to optimal. Strategies that look only for kin, non-kin or poor competitors, however, rarely do well, although recognizing competitive ability is, under most situations, better than kin recognition.

At $T-1$, among conditional rules, recognition of competitive ability (C-Comp) generally does slightly better than C-Queen or C-Kin. However, all rules do very well and are close to optimal for all values of b and s .

The cost for non-optimal behavior often substantially increases at $T-10$ (Fig. 3). Staying at all sites, which is a good rule in most instances at $T-1$, only does well with lower rates of survival. Staying only in empty sites still does well with $b \leq 0.5$, but very poorly elsewhere. All other unconditional rules do poorly with occasional exceptions, such as looking for poor competitors at $s = 1$ and $b \geq 1$. However, looking for poor competitors, though generally a poor rule, is better than the kin discrimination rules.

Conditional rules, which are almost indistinguishable from optimal at $T-1$, do substantially poorer at $T-10$, as well. As s increases, rules that do not include competitive discrimination depart further from optimality, particularly so where pleometrosis has higher benefits. Conditional response to competitive ability, however, continues to do well. Only where b is high and $0.8 \leq s \leq 0.9$ is there a higher cost.

The above analyses require a set of assumptions regarding encounter rates with empty or occupied sites, ratio of poor to good competitors, variance in competitive ability, ratio of kin to non-kin, and the degree of relatedness to kin. All of these can be varied to examine how the results of the model are affected. The methodology is the same as before, with only encounter probabilities and competition and relatedness coefficients being changed. I will not present the results in detail similar to that presented above, but instead, simply summarize how the cost of non-optimal rules changes for the three conditional rules (Table 1).

If only 10% rather than 50% of all sites are empty, all rules do worse. Discriminating competitive ability is still the best rule, doing poorly only when $b \geq 2$ and s is near 0.7–0.8. Other conditional rules fare poorly once $s \geq 0.7$.

The above analysis looks at the average competitor, one that encounters better and poorer competitors at equal rates. I examine the situation for a good competitor that encounters inferior competitors ($\alpha = 0.75$) three times more often than superior competitors ($\alpha = 0.25$) and for a poor competitor, where the encounter rates are reversed. At $T-1$ the changes for all rules are negligible, but at $T-10$ discriminating kin or competitive ability are both closer to the optimal strategy for good and poor competitors than they are for the average competitor. C-Queen is relatively unaffected. C-Comp is generally the closest to the optimal rule for all competitor qualities.

When competitive variance is reduced ($\alpha = 0.6$ or 0.4), all conditional rules are very close to optimal at $T-1$, with little to distinguish one rule as being better than the other. At $T-10$, kin discrimination is clearly superior only at $s = 1$, with high bs . Otherwise, C-Comp is still a good rule and even C-Queen is only poor with high values of both s and b .

Changing the frequency of kin encounters to 0.95 or 0.05 mimics situations where queens have low or high dispersal distances, respectively. Not surprisingly, kin discrimination becomes more valuable as the ratio kin/non-kin increases and less valuable as the ratio decreases. What is surprising, however, is that C-Comp is an equal or better rule for most values of s and b .

		RANDOM						EMPTY						
b	3.0		1	20	44	74	125		102	99	112	129	152	194
	2.5			10	30	55	101		85	81	84	98	116	153
	2.0		1	3	16	37	78		68	64	60	67	80	112
	1.5		1	3	4	18	56		51	47	43	38	45	74
	1.0		1	3	4	7	38		33	30	26	21	16	38
	0.5	1	2	5	9	14	25		17	14	11	8	6	8
	0.0	7	11	15	19	25	34		6	5	4	1		
		QUEEN						COMPETITOR						
b	3.0	10		6	15	27	57	49	34	31	25	13	1	
	2.5	16	7	5	12	22	50	48	35	25	20	10	1	
	2.0	22	15	7	9	18	43	48	37	23	15	6	1	
	1.5	28	22	16	10	13	39	48	39	29	13	3	3	
	1.0	33	30	26	21	16	38	47	42	34	22	6	8	
	0.5	40	38	37	37	37	43	48	45	41	36	28	19	
	0.0	52	54	56	59	62	69	54	55	56	55	54	52	
		KIN						NON-KIN						
b	3.0	59	45	44	41	32	25	89	79	84	87	88	96	
	2.5	59	47	39	37	30	26	82	72	69	72	72	79	
	2.0	59	50	38	33	27	28	74	67	58	56	56	63	
	1.5	60	53	44	32	25	31	67	61	54	43	39	49	
	1.0	60	56	50	41	29	38	60	56	50	41	29	38	
	0.5	61	59	58	56	53	50	53	51	48	44	39	33	
	0.0	68	71	74	77	80	84	53	54	54	53	52	49	
		0.5	0.6	0.7	0.8	0.9	1.0	0.5	0.6	0.7	0.8	0.9	1.0	
		s												
		C-QUEEN						C-KIN						
b	3.0			6	15	27	57			6	15	27	24	
	2.5			5	12	22	50			5	12	22	26	
	2.0		1	3	9	18	43			1	3	9	18	27
	1.5		1	3	4	13	39			1	3	4	13	31
	1.0		1	3	4	7	38			1	3	4	7	38
	0.5	1	2	5	8	6	8			1	2	5	8	6
	0.0	6	5	4	1					2	3	4	1	
		0.5	0.6	0.7	0.8	0.9	1.0	0.5	0.6	0.7	0.8	0.9	1.0	
		s												
		C-QUEEN						C-COMP						
b	3.0			6	15	27	24			6	15	13	1	
	2.5			5	12	22	26			5	12	9	1	
	2.0		1	3	9	18	27			1	3	9	6	1
	1.5		1	3	4	13	31			1	3	4	3	3
	1.0		1	3	4	7	38			1	2	1		8
	0.5	1	2	4	6	6	8			1		1	3	8
	0.0	2	3	4	1					3	4	4	1	
		0.5	0.6	0.7	0.8	0.9	1.0	0.5	0.6	0.7	0.8	0.9	1.0	
		s												

Table 1. The percentage costs of conditional rules as survival rate while searching (*s*) and pleometrotic benefits (*b*) vary at nest site *T*-1 or *T*-10. Blanks indicate that the rules are within 0.5% of being optimal. C, K and Q are C-Comp, C-Kin and C-Queen rules, respectively. The initial, assumed values are changed in seven ways: (1) only 10% of encountered sites are empty; (2) and (3) the searching queen is either a good or poor competitor; (4) queen variance in competitive ability is reduced; (5) and (6) either 95% or 5% of queens encountered are kin; (7) all kin are half sisters.

Initial values																	
$T-1$	$b = 3$				2	2	2	4	4	4	6	6	6	9	9	9	
	2		1	1	1	2	2	2	4	4	4	6	6	6	4	7	7
	1		1	1	1	2	2	2	1	4	4		5	5		8	8
	0		3	2	4	3	3	4	3	3	3	2	2	2	1	1	1
$T-10$	$b = 3$				6	6	6	15	15	15	13	27	27	1	24	57	
	2		1	1	1	3	3	3	9	9	9	6	18	18	1	27	43
	1		1	1	1	2	3	3	1	4	4		7	7	8	38	38
	0		4	3	5	4	4	4	1	1	1						
10% empty																	
$T-1$	$b = 3$		8	8	8	13	13	13	16	18	18	11	22	23	6	17	28
	2		5	5	5	9	9	9	9	12	12	5	16	16	2	14	20
	1		2	2	2	4	4	4	2	7	7		10	10		14	14
	0		1		5	2		7	3	1	9	4	2	9	4	3	8
$T-10$	$b = 3$		10	10	10	18	18	18	17	26	26	3	25	35		25	76
	2		6	6	6	11	11	11	9	17	17		25	25	7	35	53
	1		3	3	3	5	5	5		8	8		17	17	15	46	46
	0		3	1	7	6	3	13	10	8	20	16	14	17	6	6	8
Good competitor																	
$T-1$	$b = 3$		1	1	1	2	2	2	3	3	3	4	4	4	4	5	5
	2		1	1	1	2	2	2	3	3	3	2	4	4	1	4	4
	1		1	1	1	1	2	2		2	2		4	4		4	5
	0		4	1	6	5	1	5	2	4	4	2	2	2	1	1	1
$T-10$	$b = 3$		1	1	1	5	5	5	8	9	9	2	15	15		15	30
	2		1	1	1	3	3	3	4	6	6		10	10	4	24	27
	1		1	1	1	1	2	2		2	2		5	5	14	21	29
	0		6	2	7	5	2	5	2	2	2						
Poor competitor																	
$T-1$	$b = 3$					1	1	1	4	4	4	7	7	7	10	9	10
	2					2	2	2	4	4	4	7	7	7	9	6	9
	1		1	1	1	3	3	3	3	4	4	1	4	6		4	5
	0		1	2	2	2	2	2	2	2	2	1	1	1	1	1	1
$T-10$	$b = 3$					4	4	4	16	16	16	33	20	33	12	19	69
	2					2	2	2	8	8	8	21	17	21	5	21	51
	1		1	1	1	3	3	3	3	5	5		5	8	1	24	24
	0		2	3	3	2	2	2	1	1	1						

Table 1 continued

Low variance																
T-1	b = 3												1	1	1	
	2												2	2	2	
	1									1	1	1		3	3	
	0	3	3	2	1	2	1	1	1							
T-10	b = 3									10	10	10	13	1	34	
	2									5	5	5	3	3	19	
	1									1	1	1	3	15	15	
	0	3	1	3	1	1	1									
95% kin																
T-1	b = 3							1	1	1	1	1	1	1	1	
	2										1	1	1	1	1	
	1											1	1	4	4	
	0	1		1												
T-10	b = 3				1	1	1	2	2	2	3	2	3	20	24	
	2							1	1	1	2	2	2	17	19	
	1											1	1	14	14	
	0	1		1												
5% kin																
T-1	b = 3				1	1	1	2	5	5	1	9	9	1	12	12
	2				1	3	3	1	6	6	1	9	9	1	12	12
	1		2	2		5	5		7	7		10	10		12	12
	0		5	5		5	5	1	4	4	1	2	2			
T-10	b = 3				4	5	5	2	21	21	2	46	46		81	81
	2				1	4	4	2	15	15	1	34	34		63	67
	1		3	3		6	6		9	9		14	14	1	47	47
	0		6	6	1	6	6	1	3	3						
Half sisters																
T-1	b = 3				1	1	1	3	3	3	1	5	5		8	8
	2				2	2	2		3	3		6	6		9	9
	1		1	1		3	3		6	6		8	8		11	11
	0		4	4		4	4		2	2	1	1	1			
T-10	b = 3				3	3	3		10	10		36	36		70	79
	2				2	2	2		8	8		28	28		55	60
	1		1	1		4	4		7	7		11	11	1	42	42
	0		5	6		4	4	1	1	1						
Rules =		C	K	Q	C	K	Q	C	K	Q	C	K	Q	C	K	Q
s =		0.6			0.7			0.8			0.9			1.0		

independent of the kin ratio. C-Queen is close to optimal with a high kin ratio at $T=1$, but does poorly when kin are rare with $s > 0.7$. Likewise if queens are assumed to be half instead of full sisters ($G = 0.25$), C-Kin becomes a worse rule almost everywhere. C-Comp is almost optimal and markedly better than C-Queen with $s > 0.8$.

One limitation to this model is that group sizes of larger than two are not considered although they are commonly found in both wasps and ants (Bartz and Hölldobler, 1982; Strassmann, 1983; Rissing and Pollock, 1986). This is due in part to the 'curse of dimensionality' for dynamic programming (Houston *et al.*, 1988) in which computer limitations restrict the number of possible state variables. The greatest implication of most encountered nest sites containing two or more foundresses would be a reduction in the competitive variance across sites. Opportunities for queens to dramatically improve their competitive status would be fewer (e.g. the payoff for leaving a good competitor and finding a poor one is much higher than for leaving a group of ten good competitors and finding a group of ten poor ones). Bartz and Hölldobler (1982) model group size in relation to colony productivity and find in *Myrmecocystus mimicus* that group sizes in nature are very close to the value predicted to maximize the production of pupae per queen. They predict optimal group size to be larger when foundresses are closely related.

This model is from the point of view of the joining queen and neglects the behavior of the joined queen. Of course, a joined queen can also leave the nest site. In some cases this could lead to a conflict in that the most sought after partners might also be the most resistant to staying with other queens. Queens of poor competitive ability will always have more to gain by abandoning a shared nest. Therefore, discriminative capabilities may be more important to poor rather than good competitors.

Discussion

The dynamic optimization model presented above possibly answers why queens remain in certain nest sites when their fitness would appear to be higher in other situations (e.g. subordinates remaining in groups when solitary foundresses do better – Litte, 1977; Gibo, 1978; Queller and Strassmann, 1988). Queens may not leave because: (1) they are unlikely to survive to find another potential nest site, and (2) if they find another site, it may not be any better than the one they left.

Another general result of the model is that rules that recognize competitive ability work better than rules that recognize degree of relatedness. Varying the rate of kin encounters, the degree of sister relatedness or reducing competition variance has no effect on rule hierarchy: discriminating competitive ability is the generally better rule. A large variance in competitive ability between queens is the dominant factor favoring discriminatory ability as even kin discrimination is more likely with large competitive asymmetries.

Specific predictions about ants and wasps must take into consideration taxonomic differences in the number of nest sites encountered, survival rate between encounters, the benefit from joining a queen, and the level of competition between queens. Ant queens generally excise their wings before beginning to search for nest sites and are very vulnerable to predation and environmental stresses (Wilson, 1971). On the other hand, wasp queens are more mobile and formidable, and can search at least several days for a nest site (Evans and West-Eberhard, 1970; Strassmann, 1983). Therefore, wasp colony founding probably involves many more nest site encounters than with ants.

The benefits of pleometrosis are evident but difficult to assign an exact numerical value. Multiple foundresses have an advantage over single foundresses in Polistinae in being able to rebuild colonies after destruction by predation (Gibo, 1978; Strassmann, 1981b; Strassmann *et*

al., 1988). Furthermore, multiple foundresses produces rapid, initial growth which appears to extrapolate into larger colonies at the end of the year with a concomitant increase in the number of sexuals that can be produced. Litte (1977) found that a pair of queens produced approximately twice the worker cells of lone foundresses in *Mischocyttarus mexicanus*. In *Polistes annularis*, two queens produce ten young for every three produced by a single foundress (Strassmann, 1981a; but see Queller and Strassmann, 1988). Therefore, pleometrosis could be expected to have consistently high colony-level benefits.

For ants, success in competition between young colonies is likely to be a major benefit of pleometrosis. When initial colony densities are high, brood raiding by other colonies is a significant mortality factor. In *M. mimicus*, *Solenopsis invicta*, and *Veromessor pergandei*, pleometrotic colonies have larger initial worker broods and this increases their ability to raid other colonies. At high incipient nest densities, single queens are unlikely to succeed (Bartz and Hölldobler, 1982; Tschinkel and Howard, 1983; Rissing and Pollock, 1987). Therefore, b values could be more variable in ants than in wasps, ranging from low to high depending on initial colony densities.

Competition to dominate reproduction among pleometrotic foundresses is overt and highly aggressive in wasps, producing dominance hierarchies in which the top individual produces most of the eggs (Fletcher and Ross, 1985). Aggression between queens in ants is generally absent in the initial, cloistered stages of pleometrosis, but once the first workers mature and food is being brought into the colony, queen number is usually rapidly reduced to one (Hölldobler and Carlin, 1985; Rissing and Pollock, 1988).

Given these differences between wasps and ants, what sort of rules might they use with respect to discriminating kin and competitive ability? Wasps, with high survivorship, high benefit, intense competition and many suitable site encounters, inhabit a region where discriminating competitive ability greatly increases fitness (Fig. 3). However, as s drops to 0.9, not being able to also discriminate kin reduces a queen's fitness by over 10%. Therefore, it is predicted that wasps are very selective, especially with respect to competitive ability. Kin discrimination should also be apparent, although its effects on joining decisions should be weaker than competitive considerations.

Ants inhabit a region in the model of low to moderate survivorship, variable benefit, strong competition and fewer suitable site encounters. If benefits are consistently low, then unconditional rules like random site selection (= stay at all sites) and always stay alone are close to optimal. If benefits are consistently high, then staying only with another queen is a good rule. However, if benefits of pleometrosis vary as proposed with queen density, then these unconditional rules will work poorly and a conditional rule of stay with queens and/or empty sites depending on the value of b is an effective rule for all s and b values that might be expected. Conditional use of competitive ability discrimination could be found if queens can expect to encounter several sites. However, kin recognition rarely appears to provide any significant added benefit for increasing fitness in joining behavior. Therefore, ants are predicted to have conditional joining behavior based on variation in pleometrotic benefit. The ability to discriminate poor and good competitors may not be common but could be present in some species, particularly if most potential nest sites get occupied. Kin discrimination by foundress queens, however, should be rare if not totally absent in the Formicidae.

From relevant studies of wasp and ant pleometrotic behavior, the clearest result is with respect to kin discrimination: it seems ubiquitous in wasps and wholly absent in ants (Table 2). This is hardly a novel conclusion to those studying pleometrosis in Hymenoptera (see Rissing and Pollock, 1988). It is comforting, however, for the model to be consistent with observed data, and useful in providing a reasonable explanation as to why the two taxa behave so differently as

Table 2. Behavior of foundresses in wasps and ants. The results are summarized as to whether pleometrotic groups formed with respect to kinship (KIN), competitive ability (COMP), or density (QUEEN) of queens encountered. Dashes indicate that the variable was not tested.

	KIN	COMP	QUEEN
Wasps			
<i>Mischocyttarus mexicanus</i> (Litte, 1977)	Yes	—	—
<i>Polistes annularis</i> (Strassmann, 1983)	Yes	No?	—
<i>P. bellicosus</i> (Strassmann <i>et al.</i> , 1987)	Yes	—	—
<i>P. exclamans</i> (Allen <i>et al.</i> , 1982)	Yes	—	—
<i>P. fuscatus</i> (Klahn, 1979)	Yes	—	—
(Noonan, 1981)	Yes	—	—
(Post and Jeanne, 1982)	Yes	—	—
(Bornais <i>et al.</i> , 1983)	Yes	—	—
<i>P. gallicus</i> (Pratte, 1982)	No	—	—
<i>P. metricus</i> (Ross and Gamboa, 1981)	Yes	—	—
Ants			
<i>Acromyrmex versicolor</i> (Rissing <i>et al.</i> , 1986)	No	—	—
<i>Lasius pallitarsis</i> (Nonacs, submitted)	No	Yes	Yes
<i>Pogonomyrmex rugosus</i> (Rissing and Pollock, 1986)	—	—	Yes
<i>Prenolepis imparis</i> (N. F. Carlin, pers. comm.)	No	—	—
<i>Solenopsis invicta</i> (Tschinkel and Howard, 1983)	—	—	Yes
<i>Veromessor pergandei</i> (Rissing and Pollock, 1986)	No	—	—

regards kin. Furthermore, three studies of ants show significant increases in pleometrotic behavior as queen densities (and therefore likely intercolony competition) increase, indicating the existence of at least conditional joining behavior.

The greatest future need is to test if wasps or ants associate with respect to competitive ability. In ants, the only study available showed significant size-specific preferences in nesting *Lasius pallitarsis* queens (Nonacs, submitted). Large queens are more likely to join other queens and queens of all sizes prefer to join small rather than large queens. Size may be a potential advantage for competing foundresses. Surviving *M. mimicus* queens are larger than their eliminated partners (Bartz and Hölldobler, 1982). In *Atta texana*, larger queens survive better in

pleometrotic groups than they do alone, but smaller queens do worse in groups than alone (Mintzer, 1987).

Associating with respect to competitive ability in wasps has not been explicitly tested by observing how individuals decide between nest sites. However, queens move often between nests early in the season, perhaps looking for competitively more favorable situations. Colony usurpation by late joiners is common, which indicates that queens can improve their status (Gamboa, 1978; Gamboa *et al.*, 1986; Klahn, 1988). Furthermore, competitive ability in dominating egg-laying appears to correlate predictably with large size in *P. gallicus*, *P. metricus* and *P. fuscatus* multiple foundress associations (Turillazzi and Pardi, 1977; Dropkin and Gamboa, 1981; Noonan, 1981). However, although larger *P. annularis* queens also have a competitive advantage, group membership is random with respect to queen size (Strassmann, 1983; Sullivan and Strassman, 1984). This can be interpreted as a lack of sensitivity to competitive ability, but until individual behavior is tested, alternative hypotheses such as a competitive ideal free distribution cannot be ruled out.

In conclusion, the data clearly show pleometrosis to be more than a random process. Hymenoptera queens are selective about nest sites. The dynamic model presented here predicted this behavior based on assumptions of mutualistic benefit, survival rate in the environment, and the frequency of site types encountered. These predictions are in concordance with observed wasp and ant behavior in relation to kin. Further research is required to test if the underlying assumptions of the model are robust and if predictions of sensitivity to competitive ability hold true.

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